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The impact of forest health status on natural enemies and associates of the European spruce bark beetle *Ips typographus* (L.)

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Tiivistelmä/Referat – Abstract

The European spruce bark beetle *Ips typographus* (L.) is a severe pest of the Norway spruce *Picea abies* (Karst.). The species usually attacks weakened trees, but in a consequence of a strong abiotic disturbance event, population may increase sufficiently to threaten even healthy trees. In addition to available trees for feeding and reproduction, temperature is the most important factor limiting the damage of the pest. Limiting potential of the pest's enemies is potentially important but poorly known. There are several predator and parasite species limiting the success of *I. typographus*. These species are commonly known as natural enemies or natural enemy complex. Occurrences of these species are investigated in this study. Regardless of intensive studies about natural enemies, there are still remarkable gaps in knowledge. While natural enemies could theoretically be used to control pest populations, practical applications in forestry are in a very limited use. Mechanical methods, mainly sanitation and salvation loggings, are instead used to prevent outbreaks from escalating. These management practices prevent outbreak from spreading, although damage caused by loggings may also harm trees and expose these to pathogens. Possibility of using natural enemies as a part of pest control in forestry is considered in this study. Field study was conducted in SE Finland.

I. typographus and natural enemy complex were sampled in 2018 by means of trapping logs settled with fixed number of *I. typographus* individuals. This was conducted in three different stand classes representing different gradation phases in forests to find differences between regulating potential of enemies. Stand classes were chosen based on the visible symptoms of bark beetle infestation and disturbance history. Classes were healthy (no attack), early outbreak (first symptoms and increased pest population) and declined outbreak (earlier outbreak, pest already declined near endemic level). Trapping logs with settled *I. typographus* were allocated to these classes, and insects emerging from trapping logs were later collected for sampling in sealed funnel traps. *I. typographus* population level was simultaneously monitored using pheromone traps. Differences between insect occurrences in different stand classes were statistically analysed by Kruskal-Wallis test with 0.05-level of significance for each identified enemy species and families. Spearman correlation was also used to detect any possible relations between different enemy species.

Predators emerging from the logs were identified to six coleopteran families. Species were *Thanasimus formicarius* (Cleridae)*, Plegaderus vulneratus* (Histeridae)*, Epuraea spp.* (Nitidulidae)*, Rhizophagus spp.* (Monotomidae) and from Staphylinidae *Quedius plagiatus, Nudobius lentus, Phloeonomus spp., Leptusa spp.* and *Placusa spp.* Family Elateridae was inspected as a single tested group. Predatory flies and parasitic wasps also emerged from the logs, although these were excluded from the current study. Three species had significant preference to certain outbreak classes. *P. vulneratus* proved most promising regulator in this study. It reproduced rapidly already during the first year of infestation. *T. formicarius* had significant preference for stand class, but failed to occur in sufficient numbers during the first year of infestation to have impact on the *I. typographus* population. Staphylids *Phloeonomus spp.* were very common at all stand classes but preferred healthy class. For both *P. vulneratus* and *Phloeonomus spp.* preferences for stand classes were significant, but the regulation effectiveness of these species is relatively unknown.

Results suggested that limited resources in the healthy class, similar to managed forests forces both bark beetles and predators into same space, potentially increasing mortality. This result was observed by increased total numbers of beetles in the trapping logs of healthy class in comparison to outbreak classes, while simultaneously prey-predator ratio was also lower. This means that in addition to removing resources, sanitation loggings could also have increasing effect on enemy induced mortality. Small amount of deadwood potentially sustains higher endemic population of enemies, potentially increasing stands resistance to further insect induced disturbances. While some enemies were more common at the declined outbreak class, this claim was not supported by this study.

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Tiivistelmä/Referat – Abstract

Kirjanpainaja *Ips typographus* (L.) on kuusen *Picea abies* (Karst.) merkittävä tuholainen. Laji iskeytyy yleensä heikentyneisiin puihin, mutta voimakkaan abioottisen häiriön seurauksena populaatio voi nousta riittävästi uhatakseen jopa täysin terveitä puita. Saatavilla olevien ravinnoksi ja lisääntymiseen käytettävien puiden lisäksi lämpötila on tärkein tuholaisen aiheuttamia tuhoja säätelevä tekijä. Tuholaisen luontaisten vihollisten merkitys on mahdollisesti tärkeä, mutta huonosti tunnettu. Moni saalistaja- ja loislaji rajoittaa kirjanpainajan menestystä. Näistä lajeista puhutaan yleensä luontaisina vihollisina. Tässä työssä tutkitaan näiden lajien esiintymistä. Luontaisista vihollisista tehdystä intensiivisestä tutkimustyöstä huolimatta tiedoissa on vielä huomattavia aukkoja. Vaikka luontaisia vihollisia voitaisiin teoriassa käyttää tuholaisen kannansäätelyssä, sovelluksia ei käytännössä juurikaan ole. Sen sijaan mekaanisia toimenpiteitä, pääosin sanitaatiohakkuita ja yksittäisten kuolevien puiden poistoa hyödynnetään tuhon laajenemisen estämiseksi. Nämä hoitotoimenpiteet estävät hyönteistuhoa leviämästä, mutta hakkuut aiheuttavat korjuuvaurioita ja altistavat puita taudinaiheuttajille. Tässä työssä pohditaan luontaisten vihollisten mahdollista käyttöä osana tuholaisen torjuntaa. Kenttätutkimus suoritettiin Kaakkois-Suomessa.

Kirjanpainajia ja luontaisia vihollisia kerättiin aineistoa varten vuonna 2018 ansapuilla, joihin oli istutettu valmiiksi vakiomäärä kirjanpainajayksilöitä. Tämä tapahtui kolmeen eri tuholuokitukseen jaetuilla koealoilla, jotka edustivat kirjanpainajan joukkoesiintymän eri vaiheita. Tällä pyrittiin löytämään eroja luontaisten vihollisten potentiaalisesta kyvystä säädellä kirjanpainajan kantaa. Koealaluokitukset valittiin puissa näkyvien oireiden ja tuhohistorian perusteella. Luokat olivat terve (ei oireita), varhainen hyönteistuho (ensimmäiset oireet ja kohonnut tuholaiskanta) ja väistyvä hyönteistuho (aikaisempi tuho, tuholaisen kanta jo laskenut lähelle lähtötilannetta). Kirjanpainajien täyttämät ansapuut jaettiin koealoille, ja myöhemmin sinetöidyistä ansapuista ilmaantuvat hyönteiset kerättiin suppilon muotoisen ansajärjestelmän avulla. Kirjanpainajan kantaa seurattiin samanaikaisesti feromoniansoilla. Erot määritettyjen hyönteislajien ja heimojen esiintymisessä eri koealaluokkien välillä analysoitiin tilastollisesti Kruskal-Wallis testillä 0.05- merkitsevyystasolla. Myös Spearman-korrelaatiota käytettiin eri vihollislajien välisten vuorovaikutussuhteiden havaitsemiseksi.

Ansapuista ilmaantuvat saalistajat määritettiin kuuluviksi kuuteen eri kovakuoriaisheimoon. Tunnistetut lajit olivat *Thanasimus formicarius* (Cleridae), *Plegaderus vulneratus* (Histeridae), *Epuraea spp.* (Nitidulidae), *Rhizophagus spp.* (Monotomidae) sekä Staphylinidae-heimosta *Quedius plagiatus, Nudobius lentus, Phloeonomus spp., Leptusa spp.* ja *Placusa spp.* Myös Elateridae -heimo käsiteltiin yksittäisenä ryhmänä. Ansapuista ilmaantui myös saalistavia kärpäslajeja sekä loispistiäisiä, jotka jätettiin kuitenkin tutkimuksen ulkopuolelle. Kolmen luontaisen vihollisen havaittiin tilastollisesti merkitsevästi esiintyvän runsaampina tietyissä koealaluokissa. *P. vulneratus* vaikutti tutkimuksen perusteella lupaavimmalta kannansäätelijältä. Se lisääntyi runsaana jo ensimmäisenä vuonna tuhon synnystä. *T. formicarius* esiintyi runsaimpana terveellä koealaluokalla, mutta tuhon ensimmäisen vuoden aikana liian vähälukuinen vaikuttaakseen kirjanpainajan populaatioon. *Phloeonomus*-suvun lyhytsiipiset olivat yleisiä kaikissa koealaluokissa, mutta suosivat tervettä koealaluokkaa. Sekä *P. vulneratus* että *Phloeonomus spp.* olivat selkeästi yleisempiä tietyssä koealaluokassa, mutta näiden lajien säätelykyky ja merkitys ovat melko heikosti tunnettuja.

Tulokset vihjaavat, että rajallinen määrä resursseja terveessä koealaluokassa kuten myös talousmetsissäkin pakottaa sekä kirjanpainajan että saalistajat samaan tilaan, mahdollisesti lisäten kuolleisuutta. Tämä näkyi korkeana määränä kuoriaisia terveen koealaluokan ansapuissa, kun samalla tuholainen/saalistaja-suhde oli matala. Tämän perusteella sanitaatiohakkuut voisivat myös lisätä vihollisten aiheuttamaa kuolleisuutta. Myös pieni määrä kuollutta puuta voisi potentiaalisesti pitää luontaisten vihollisten määrän koholla, vahvistaen metsikön vastustuskykyä tulevia hyönteistuhoja vastaan. Vaikka osa vihollisista olikin yleisempiä väistyvän hyönteistuhon koealaluokassa, tämä tutkimus ei tue tätä väitettä.

Avainsanat – Nyckelord – Keywords
Ips typographus, kirjanpainaja, luontainen vihollinen, metsänhoito, metsäkuusi, metsätuholainen

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1. INTRODUCTION

1.1. Forest health and bark beetle outbreaks

Biotic damage of pests and pathogens is an important cause of tree mortality, often succeeding abiotic damage. Large-scale damage caused by bark beetles (Curculionidae: Scolytinae) is mentioned in the manuscripts of as early as late eighteenth century (Saalas 1919). Millions of hectares are affected by bark beetle infestations in North America (Kirisits et al. 2012), and Europe (Grégoire and Evans 2007). These bark beetle outbreaks have been studied starting from the nineteenth century (Saalas 1949, Dajoz 2000). Bark beetles are often linked to storm damage, but can also benefit from drought or pathogen ridden trees (Goheen and Hansen 1993, Angst et al. 2012, Marini et al. 2017). While bark beetles have been a target for studies for almost two centuries, damage potential caused by changing climate makes estimating the magnitude of the damage difficult in the future (Bentz et al. 2010, 2019, Jönsson et al. 2011).

Forest pests can be divided to primary and secondary pests, depending on whether they can cause damage without exogenous disturbance. This dichotomical categorization between primary and secondary pest is not feasible in the case of bark beetles (Kangas 1950). Tree vigour governs how well bark beetles succeed in overcoming the trees defences (Raffa and Berryman 1983, Mulock and Christiansen 1986). This attribute makes bark beetles generally secondary pests. This classification is not simple, as eruptive nature of certain bark beetle species makes them capable of swarming in sufficient numbers to damage healthy trees, seemingly becoming primary pests in high population densities (Saalas 1949, Berryman 1982, Raffa and Berryman 1983). Dichotomy between primary and secondary pest is therefore not only the attribute of the insect, but also affected by the health status of the forest stand. Forest health is therefore an important factor alongside a vigour of a single tree in comparison to landscape level scale (Trumbore et al. 2015). Prevention of damage and understanding the disturbance dynamics of insects will therefore require knowledge about both ecology of the pest and predictors for stand health. This opens a question concerning the regulating effect of the predators and parasites. While the pest itself is strongly affected by forest health, are these natural enemies equally limited by the stand structure?

1.2. *Ips typographus* L. – The European spruce bark beetle

The European spruce bark beetle (*Ips typographus* L.) is a Coleopteran species with native distribution in vast areas of Europe and Asia (Christiansen and Bakke 1988). This beetle from subfamily Scolytinae (bark beetles) is economically the most significant insect pest of Norway spruce (*Picea abies*, L. Karst.) in its Eurasian distribution (Christiansen and Bakke 1988, Wermelinger 2004). While the species is pest only on spruce, it can be occasionally met in pine, fir and larch (Saalas 1949, Dajoz 2000). The species prefers weakened trees and does not seem to be as capable of attacking healthy trees as other globally significant bark beetles (Kärvemo and Shroeder 2010). Total extent of the damage is difficult to evaluate. On average, 2.9 mill. cubic meters of wood have been estimated to be damaged by bark beetles annually in Europe (Schelhaas et al. 2003). Tree vigour seems to be the most important trait affecting the risk of bark beetle infestation (Raffa and Berryman 1983, Mulock and Christiansen 1986). The damage is usually a follow-up cause from previous disturbances in a forest, such as wind-felled trees (Saalas 1949, Komonen et al. 2011, Wermelinger et al. 2013). After such disturbances, population may reach threshold, after which the species may pose a threat to completely healthy trees (Berryman 1982). All other stress factors, such as drought may also affect the trees capability to resist infestation (Netherer et al. 2015, Marini et al. 2017). At high population densities, trees are at risk of being overwhelmed by insects. Even in endemic levels, *I. typographus* can kill trees on the susceptible locations like edges of clear cuts (Christiansen and Bakke 1988, Hedgren and Schroeder 2004). While pest itself may prove to be lethal for its host, it may also damage trees by transmitting several fungal pathogens, usually different blue-stain fungi (Hornvedt et al. 1983, Solheim 1988, Kirisits 2007, 2010, Hofstetter et al. 2015, Linnakoski and Forbes 2019). Attack on the trees occurs in synchronous swarming events and is controlled by volatile substances emitting from the tree and aggregation pheromones formed in the beetle hindgut (Bakke 1973, Bakke and Kvamme 1981, Dajoz 2000).

Overwintered adults begin mass flight once temperature rises above 16°C (Lobinger 1994, Öhrn et al. 2014). The Species prefers temperatures over 20°C (Annila 1969, Wermelinger 2004), 30°C being upper limit for the flight (Lobinger 1994). The species usually attacks trees with thicker bark, being over 10 centimetres in diameter at breast

height (Hedgren and Schroeder 2004). The species bores chambers in lower part of bark and phloem, where they oviposit. Up to three females for each male, rarely four, are gathered to same nuptial chamber, forming polygamous gallery (Wermelinger 2004, Öhrn et al. 2014). Development rate from egg to adult is mostly dependent on warmth (Wermelinger and Seifert 1998, Wermelinger 2004), but also on intraspecific competition (Anderbrant et al. 1985, Anderbrant 1986). Development requires minimum of 8.3°C to begin (Wermelinger 2004). In optimal conditions, life cycle is finished in less than three weeks (Wermelinger and Seifert 1998). Adult beetles often leave galleries after laying eggs, re-emerging and reproducing again in a new location. This behaviour generates sister broods (Martinek 1956, Annila 1969). Significance of the sister broods may vary annually, but these accumulate great portions of *I. typographus* damaged trees (Bakke et al. 1977b, Mezei et al. 2017). Most adults are expected to overwinter under bark of host tree in Central Europe (Hardig and Ravn 1985) and in litter in the northern parts of Central Europe and Scandinavia (Austarå and Midtgaard 1986, Weslien 1992a). This pattern is most likely due to the differences on snow-cover and minimum temperatures of winter. This is supported by the fact, that the same phenomenon is seen with differences between temperatures caused by the topography (Wermelinger and Seifert 1999, Kasumović et al. 2019).

Similar to the overwintering habits, lifecycle and voltinism of spruce bark beetle depend on accumulated temperature. In Northern Europe, univoltinism is more common (Annila 1969, Öhrn 2014), with only exceptional conditions allowing second generation to occur. In general, Norway, Sweden and Finland (Annila 1969, Schroeder 2007) have univoltine populations, while Denmark (Harding and Ravn 1985) and Central-Europe (Germany, Poland and Austria) are bivoltine dominant in lowlands (Christiansen and Bakke 1988, Jakoby et al. 2019). Countries further south may encounter third generation (Netherer 2003, Netherer and Nopp-Mayr 2005, Jönsson et al. 2009, 2011, Jakoby et al. 2019). Since warmth is governing characteristic in *I. typographus* development, alterations in temperature due to topography affect voltinism and development speed (Wermelinger and Seifert 1998, Gall and Heimgartner 2003). Therefore, dichotomy between uni- and multivoltine areas is not only matter of latitude. Number of generations is not stable either, as Scandinavian univoltine populations can adapt to environmental cues and have already become bivoltine if conditions are met (Jönsson et al. 2009). Effects of the

warming climate have potential to extend the area of bivoltine reproduction (Jönsson et al. 2011, Bentz et al. 2019).

I. typographus prospers in trees until the resources deplete. Once the suitable space and nutrition runs out, lack of easily obtainable resources causes declining of *I. typographus* populations. Thus bark beetle body size has been smaller and reproductive success weaker in higher population densities (Anderbrant et al. 1985, Faccoli and Bernardinelli 2011), which would imply strong intraspecific competition. It can be seen as the most important factor, when wind-damaged trees run out and beetle population starts to shift into healthy standing trees (Komonen et al. 2011). It is suggested, that this population shift starts several years after the abiotic disturbance that originally induced the outbreak (Mezei et al. 2011). Symptoms visible earlier than that on the trees are primarily cause of stress and damage from that disturbance making trees vulnerable for endemic populations (Gall and Heimgartner 2003). While bark beetles seem to prefer dead or dying trees with lesser defensive response, there are some opposing results indicating that reproductive success is greater on the standing trees (Hedgren and Schroeder 2004). Hedgren and Schroeder (2004) speculated that this phenomenon is due to more optimal humidity, implying that fallen dead trees desiccated too fast. Numbers and reproductive success of *I. typographus* offspring decrease as population density increases (Sallé et al. 2005, Faccoli and Bernardinelli 2011). There is high propability that intraspecific competition eventually collapses the population unless new exogenous disturbances occur.

1.3. Monitoring the spruce bark beetle

Pheromone is a term for substance used in communication between insect individuals (Karlson and Lüscher 1959). Aggregation pheromones of the bark beetles are plant originated substances, which change their form in the insect's digestive track (Dajoz 2000). These pheromones can be artificially mimicked and are widely used to monitor population of *I. typographus* by collecting individuals in masses. Monitoring can help to decide whether management actions are needed to prevent insect damage (Schroeder 2013). It is often referred that risk limit for bark beetle damage is about 5000 captured individuals in a single trap (Niemeyer 1992) or 15 000 individuals in a group of three traps (Weslien et al. 1989) in one summer. In Norway, trapping was attempted in a larger scale in order to reduce the overall pest population (Bakke 1989). While this kind of

damage mitigation is possible, it must be first economically justified. Trapping campaign in Norway 1978-1982 was estimated to cost about 50 mill. NOK / six mill. U.S. dollars (Bakke 1989). Even as mass trapping method has been estimated to help lower the population of *I. typographus* (Faccoli and Stergulc 2008), true impact of this campaign on the *I. typographus* population is still unclear. The idea of lowering the pests' population with traps is therefore usually disregarded. Norway for example has nowadays only hundreds of traps for regional monitoring (Galko et al. 2016). Pheromone traps themselves do not prevent any damage unless deployed extensively, and are more often considered supplementary to other methods of sanitation (Niemeyer 1997).

There is a plentiness of different pheromone trap types. No statistically significant difference between catch rates of the different trap types have been proven (Galko et al. 2016), which implies that used pheromones and trap placement are more relevant. In addition to artificial traps, pheromones have been used in trapping logs for additional attracting effect (e.g. Weslien 1992b). Treating trapping logs with pesticides also has similar effect compared to pheromone traps, killing bark beetles and associates that are attracted to pheromone bait (Lubojacký and Holuša 2011). Most important components for *I. typographus* pheromone lures are methylbutenol, cis-verbenol and ipsidienol (Bakke et al. 1977a). Volatiles emitting from trees, like monoterpenes and ethanol, have also baiting effect (Bakke and Kvamme 1981). Several other potentially important pheromone components have been identified from the hindgut of the beetle, but Subtracting methylbutenol and cis-verbenol lower the total catch of trapping (Schlyter et al. 1987). Pheromone trapping is widely used and tested method in monitoring the population and assessing the risk. Trapping correlates well with the damage expected within the same summer (Bakke 1985, Weslien et al. 1989). Main source of error for population estimate is suboptimal trap placement causing variation between individual traps (Scroeder 2013). Beetle population can also cause damage simultaneously before the risk indicated by the traps is noted, making relevant predictions of damage difficult (Weslien 1992b). Pheromone trapping is therefore working better as a regional system instead of single stand predictor (Niemeyer 1992).

Methods that are more modern include remote sensing health of stands and individual trees. The novel way of remote sensing is using satellite and airborne imagery. This can be done by assessing leaf area (e.g. Coops et al. 2009) or changes in the crown colour

(e.g. Näsi et al. 2015). Green attack, phase without visible symptoms, can continue weeks before crown colour changes (Näsi et al. 2015). Therefore it would be highly beneficial to generate methods of early detection before symptoms are visible to human eye. This technology is in development, and first results of hyperspectral imaging have been encouraging (Lausch et al. 2013, Näsi et al. 2015). While bark beetle population cannot be assessed through remote sensing, insect damage and tree symptoms can be detected relatively reliably. In the near future, remote sensing tools can replace some of the labour-intensive actions (Näsi et al. 2018).

1.4. Natural enemies and associates – Overview

There are several parasitic, predatory or otherwise antagonistic species, which affect population of *I. typographus*. This group as a whole is known as natural enemies or natural enemy complex. This complex is vast, and therefore the current study focuses mainly on the predatory interactions. *I. typographus* also plays an important role as a facilitator and ecosystem engineer (Borkowski and Podlaski 2011). The spruce bark beetle acts as a keystone species (Müller et al. 2008), supporting range of saproxylic species in addition to its enemies. Even cautious estimates are over 140 associated arthropod species in Europe (Weslien 1992a). The natural enemy complex of spruce bark beetle is relatively well known, with several summaries available (e.g. Mills 1985, Kenis et al. 2004, Wegensteiner et al. 2015). This knowledge still has gaps and contradictions to solve. Especially impact of the less known enemies and their respond to management practises have remarkable gaps. Role and impact of several enemies also vary between studies. This gap in knowledge is important deficiency, as we do not know if less well-known species would have greater impact on the pest, if stands were managed in a different way.

Enemies can be divided by their feeding habits into predators, parasites and parasitoids. Predators can be furthermore divided into specialist predators, generalist predators and true omnivores (Coll and Guershon 2002), depending whether predator preys on single species, switches between different prey species (generalist predator) or between animal and plant/fungal material (true omnivore). All these feeding strategies have been met among predators of bark beetles, although predators seem to be very often generalists (Johansson et al. 2007). This means that all bark beetles are potential prey, *I. typographus*

simply being in many cases the most common. Parasitoids are in comparison very specific to their prey. In order to ensure host being present, parasitoids emerge later than host (Wermelinger et al. 2012). Parasitoids are very efficient in regulating populations but are limited to one prey in their lifecycle. This makes them less mobile and capable of attacking only one life stage of bark beetle (Khanday et al. 2018). There are also exceptions to this, e.g. parasitoid *Tomicobia seitneri* (Ruscha, 1924) is bivoltine (Georgiev and Takov 2005). Other limiting factors for bark beetle success are intraguild omnivory (larger phytophagous species occasionally feeding on their smaller competitors) and competition (Coll and Guershon 2002). Good example of intraguild omnivory is cerambycid beetle larvae competing on the space and occasionally feeding on scolytid larvae (Dodds et al. 2001).

Natural enemies have different strategies finding their prey. For the omnivores and generalist predators, bark beetles are most likely consumed when available. Many species are known to actively seek their prey. Kairomone effect, predator tracking pheromones of the prey to locate them, has been commonly observed among many predators of *I. typographus* (Weslien and Shroeder 1999, Kenis et al. 2004). Predators also actively seek their prey in places where the fumes of several chemical compounds emerge from the damaged trees (monoterpenes such as α-pinene and ethanol from decaying wood) (Bakke and Kvamme 1981, Schroeder and Weslien 1994).

1.5. Natural enemies and antagonists– impact on *I. typographus*

While natural enemy complex is relatively well known, their impact on population level and reproduction of *I. typographus* varies between studies. Enemy species of different bark beetle species differ, and a total enemy impact on population mortality has varied between 24%-97% (Lawson et al. 1996). Effect of the enemies on the reproductive success and predation of *I. typographus* larvae has varied greatly as well. Commonly estimated impact has been low, concentrating on single species in exclusion experiments. In Mills' (1985) experimental setup, predatory *Thanasimus formicarius* (Linnaeus, 1758) larvae caused only 18% brood mortality. This is an example of a low impact. As predators are not guaranteed to find prey on early phases of the outbreak, impact on the first generation of bark beetles may remain modest. On the contrary, enemies may have great impact if they find prey early enough. Weslien (1992a) showed that *I. typographus* brood

in interaction with predators was reduced by 83% more than in logs protected from predators by caging. Predation may therefore be a significant factor in population control in the epidemic phase of the pest. Differences in enemy impact between experiments may be a result of different species, experimental conditions or pure coincidence. Due to differences between results, impact is hard to estimate other than case-wise (Wermelinger 2004).

I. typographus has strong competitive advantage over other phloem feeders due to strong pheromone communication (Weslien 1994), which means that potential competitors for nutrition and space are insignificant compared to intraspecific factor. Main competitors are other bark beetles, of which many are secondary pests. Common examples are *Hylurgops palliatus* (Gyllenhal, 1813*)* and *Pityogenes chalcographus* (Linnaeus, 1761), of which the latter is also considerable pest in Central Europe (Rudinsky 1962, Niemeyer 1997). It is often encountered in the same space as *I. typographus* (Dajoz 2000), althought it prefers smaller diameter trees than *I. typographus* (Nitterus et al. 2004). Field experiment of Weslien (1992a) signals that competing bark beetle species occupy space a lot later than *I. typographus*, even benefitting from the leftover space in *I. typographus* infested trees. In relation to many other bark beetles, *I. typographus* often colonises weakened trees or even healthy trees as a primary pest. Many other bark beetles colonize remaining space soon after, resulting in higher species richness in later years (Kärvemo et al. 2017). This proves that other bark beetles are hardly competing for the same niche. On the contrary, cerambycid beetles are using similar niche and are therefore potential antagonists of bark beetles (Schroeder and Weslien 1994, Dodds et al. 2001). These long-horned beetles have significantly slower lifecycle and are fewer in numbers than bark beetles. Most likely these reduce suitable space for bark beetle broods in the following year at earliest.

The significance of early predation is still somewhat questionable, since temporal differences in occurrences of the spruce bark beetle and predators happen. For example, bark beetles can produce multiple generations in one summer (bi/trivoltinism), while their predators may be limited to one (Nicolai 1996, Kenis et al. 2004). This allows bark beetles to reproduce faster than their predators. Some predatory species may even take longer than one summer to mature. Ant beetles, usually the most important predators mentioned, belong to this category in Scandinavia (Schroeder 1999). This results delayed

development of adults capable of migrating from one forest stand to another. Thus, predators will be able to follow up its prey species only after a longer period of time. In addition to temporal differences, natural enemies are required to find prey before its reproduction may begin, either by accidental encounter or through actively following pheromone trail of the prey. Prey may gain a head start in reproduction. Therefore, reduction of bark beetle population by predators may take few years to have a significant effect (Schroeder 2007). For example, Saalas (1949) noted in his experiments in 1919-1922 that tree mortality after the wind disturbance was in its maximum in the second year after the initial storm damage. Enemies and lack of fresh deadwood are expected to decrease the population after that. This time lag reduces the effectiveness of the natural regulation. This makes endemic population of the enemies' an important factor in pest regulation, as abundance of enemies supposedly increases the chances of prey and predator to meet. While lag in population reduction has been an accepted theory for a long time, opposing results exist with synchronous population growth of both prey and its enemy occur (e.g. Wermelinger et al. 2013). Some case studies have had predators to have reducing effect already on the early phases of bark beetle gradation (Reeve 1997).

1.6. Natural enemies – species

1.6.1. Thanasimus spp. - Ant beetles

Ant beetles (*Thanasimus spp*., Cleridae) are usually mentioned as the most significant Coleopteran predators of spruce bark beetle (e.g. Mills 1985, Weslien and Regnander 1992). Bark beetle predation by this family has been recognized very early on the nineteenth century (Schaufuss 1892, Dajoz 2000). Genus preys on several bark beetle species on different conifers and sometimes on deciduous trees (Gauss 1954). Slim shaped larvae lives under bark, feeding on bark beetle larvae. Adults on the contrary, are too large to chase bark beetles in phloem, but instead prey on adult bark beetles seeking for potential brooding sites (Herard and Mercadier 1996). In literature, Clerid beetles from genus *Thanasimus* have been one of the few groups of predators with significant effect on reproductive success of *I. typographus* (Weslien and Schroeder 1999, Hilszczański et al. 2007). This is most likely due to high voracity as a larva, requiring tens of bark beetle larvae as prey before emerging as adult (Mills 1985, Dippel et al. 1997). These species are capable of reproducing relatively fast when favourable

conditions are met. Average number of over hundred eggs per female have occurred in the studies (Weslien and Regnander 1992, Dippel et al. 1997). Females can also oviposit eggs through the whole summer (Gauss 1954), potentially distributing offspring into larger area. *Thanasimus formicarius* (Linnaeus, 1758) and *Thanasimus femoralis* (Zetterstedt, 1828) have presented clear kairomone effect (Bakke and Kvamme 1978, 1981, Schlyter and Lundgren 1993). Therefore these species are captured in high numbers in the pheromone traps luring *I. typographus* (Valkama et al. 1997, Galko et al. 2016). The genus is also exceptional compared to other predators, since it can prey on both adults and larvae of *I. typographus*, and probably on eggs too. In the temporal studies most of the *Thanasimus* have emerged very early in spring (Wermelinger et al. 2012). *T. formicarius* is also commonly met in pines (Hilszczański et al. 2007), preying also on other scolytid species. While larvae live underneath the spruce bark, these are claimed to be incapable of pupating in spruce (Warzée et al. 2006, Thomaes et al. 2017). Studies indicate that the species pupates outside of the spruce on the ground level (Weslien 1994).

Life cycle of commonly studied species *T. formicarius* varies between uni- and semivoltine in Central Europe (Wermelinger et al. 2012), while in further north life cycle is usually always semivoltine (Schroeder 1999). In Scandinavia, *T. formicarius* commonly overwinters as a pupa (Ye 1998) or perhaps even as a larva. The species finalizes its lifecycle and emerges on early spring (Wermelinger et al. 2012). It is suggested that females are not ovipositing during the first year (Ye 1998). This means that the species lives for almost three years, during which it consumes significantly more prey than most other antagonists. *T. formicarius* is present in Eurasia within a similar range as *I. typographus* (Weslien and Regnander 1992). Several other species of *Thanasimus* and Cleridae are known enemies of bark beetles e.g. in North America (Wegensteiner et al. 2015) but are left out of this study since they have no current effect on *I. typographus*. *I. typographus* is a potential invasive pest for North America, making those species relevant for future studies.

1.6.2. Histeridae – Histerid/clown beetles

All of the histerid beetles encountered in the bark beetle galleries are claimed to be predators, but their impact is unknown (Dajoz 2000). Most common predators from family Histeridae belong to genera *Platysoma* and *Plegaderus* (Kenis et al. 2004,

Wegensteiner et al. 2015). Certain species are also encountered as a detrivore or forager in the galleries of bark beetles (Herard and Mercadier 1996). While genus *Platysoma* is important enemy of the bark beetles (e.g. Shepherd and Goyer 2005), these are usually enemies of the bark beetles living in different pine species. Of two commonly mentioned predators on spruces, *Plegaderus vulneratus* (Panzer, 1797) seems to be a common associate on the whole distribution of *I. typographus*, while *Paromalus parallelopipedus* (Herbst, 1792) is usually absent in Scandinavian studies (e.g. Martikainen et al. 1999, Weslien and Schroeder 1999). *P. parallelopipedus* is also near absent in higher elevations of Central Europe (Wermelinger 2012), which means distribution is most likely limited by temperature. Other species from these genera may have similar feeding habits, but these two species are the ones mentioned in literature with *I. typographus.* Due to small body size of the species encountered in galleries, histerids are mainly predators of eggs and larvae. *Plegaderus* species have been proven to feed on scolytid eggs (Nuorteva 1956). *Plegaderus*-individuals have also been encountered in the galleries after eggs have already hatched (Schroeder and Weslien 1994), implying also consumption of bark beetle larvae. Potential prey also includes other soft larvae, e.g. Diptera (Saalas 1949). Adult histerids of these genera commonly emerge during early spring (Wermelinger 2012). Adults either overwinter in the galleries or mature in spring. On the contrary, Weslien (1992) observed, that *P. vulneratus* had barely inhabited the logs within eight weeks of *I. typographus* flight. While this implies that species is on flight relatively late in Northern Europe, populations in Central Europe have been overwintering and emerging in greater numbers in spring (Wermelinger 2012).

In addition to spruce and pine, histerids are encountered in deciduous trees. *Plegaderus vulneratus* and *Paromalus parallelopipedus* are dependent on infested trees, and wide variety of potential host tree and prey species makes them less vulnerable to fluctuations in prey populations (Hilszczański et al. 2007). While impact of the *P. vulneratus* on bark beetles is not well known, these can be relatively numerous at the bark beetle galleries (e.g. Hedgren and Schroeder 2004). Wide host tree range also implies that *P. vulneratus* is generalist, feeding on larvae of other scolytid species and insect orders.

1.6.3. Nitidulidae – Sap beetles

Sap beetles can be encountered in flowers eating nectar or in the deciduous tree trunks feeding on the sap. Many species on the contrary live underneath bark as a larva. While adults are often met on the open space like meadows, studies indicate that most of these species prefer laying their eggs in the standing trees or trees on the more closed canopy (Hedgren and Schroeder 2004, Johansson et al. 2007). Nitidulid beetles seem to leave trees soon after maturing, as larvae can be very common while adults are not as abundant in galleries (Weslien 1992a). This family seems to be difficult to classify, and not often clearly identified as a predator or omnivore.

Nitidulid beetles respond on different resinous volatiles emitted by damaged trees. Potentially predatory genera attracted by these chemical compounds include *Epuraea*, *Glischrochilus* and *Pityophagus* (Voolma and Sibul 2001). Several species are identified as an enemy of the spruce bark beetle (Mills 1985, Kenis et al. 2004, Wegensteiner et al. 2015), but their role and importance are still considered unclear in many studies. Genus *Epuraea* is most commonly met in bark beetle galleries. Many species in this genus have been proven consuming scolytid eggs (Nuorteva 1956). There are 34 *Epuraea*-species met in Finland (Rassi et al. 2015), of which at least six were mentioned to prey on *Ips*-species (Kenis et al. 2004, Wermelinger et al. 2012). More species are likely to fill the same niche as these six species.

1.6.4. Rhizophagus spp. – Root-eating beetles

There are a few species of monotomid beetle genus *Rhizophagus*, which are considered voracious. Best known examples most likely being generalist predator *R. ferrugineus* (Paykull, 1800) and specialist predator *R. grandis* (Gyllenhal, 1827) (Kenis et al. 2004). Almost all monotomid species live under bark. Very common associates of *I. typographus* are *R. dispar* (Paykull, 1800) and *R. depressus* (Fabricius, 1792). There has been reasonable doubt on whether *R. dispar* uses bark beetles as a frequent prey (Kubisz 1992), while at least some sources have documented occasional predation of *I. typographus* larvae (Kenis et al 2004, Johansson et al. 2007). Often it has been referred as mycetophagous (Merlin et al. 1986, Weslien 1992a), but also seen as a scavenger (Weslien 1992a, Hedgren and Schroeder 2004). It is also common predator in corridors

of bark beetle *Hylurgops palliatus* (Dajoz 2000). Usually it is still mentioned among the more certain predators, and it would be excessive to automatically assume otherwise. Diet of *R. depressus* has also been debated. Species has survived with fungal diet and have even been recorded to become obligate saprophage in later larval instars (Herard and Mercadier 1996). These studies would imply that the genus is mainly omnivorous, with some influence on bark beetles. Omnivory behaviour and scavenging is supported by the fact, that genus is present relatively late after *I. typographus* has inhabited trees (Weslien 1992a). Despite the mixed results in the earlier studies, the whole genus *Rhizophagus* is treated as a natural enemy in the current study.

1.6.5. Tenebrionidae – Darkling beetles

Species of Tenebrionidae are not usually considered predatory. Genus *Corticeus* (previously *Hypophloeus*) on the contrary is considered a predator of bark beetle larvae (Herard and Mercadier 1996, Hedgren and Schroeder 2004, Wegensteiner et al. 2015, Khanday et al. 2018). Adult beetles are commonly found in the galleries of *I. typographus*, preying on larvae.

1.6.6. Staphylinidae – Rove beetles

Staphylinidae is a very large family. It includes many species living under spruce bark, few of which have been identified at least as a generalist predator or omnivore. While role of the most staphylid species is unknown, some of them most certainly use bark beetles as occasional prey (Dajoz 2000).

Species rich staphylid beetle subfamily Aleocharinae includes species living in the galleries of bark beetles. Subfamily is found already on the very early colonization phase of bark beetles (Weslien 1992a). Feeding habits of this subfamily are either considered unclear (Weslien 1992a, Weslien and Schroeder 1999, Hedgren and Schroeder 2004) or omnivorous (Kenis et al. 2004). Common Staphylinids from Aleocharinae encountered in bark beetle galleries include genera *Placusa*, *Leptusa* (Weslien 1992a, Weslien and Schroeder 1999) and *Phloeopora* (Weslien 1992a, Wermelinger et al. 2012).

On the very common genus *Phloeonomus* (Omaliinae), there are three species met in Finland (Rassi et al. 2015), of which all have been mentioned in some literature to prey on *Ips* species. *P. pusillus* (Gravenhorst, 1806) is an example of a very common species, which has been mentioned to prey on bark beetle larvae (Kenis et al. 2004). In literature, *P. sjoebergi* (Strand, 1937) is referred as a predator more often than others (e.g. Weslien 1992a, Kenis et al. 2004, Johansson et al 2007).

Nudobius lentus (Thomson, 1860) and *Quedius plagiatus* (Mannerheim, 1843) belong to subfamily Staphylininae. Both species are common and relatively large predators, whose slim shape allows movement in bark beetle galleries. These are encountered under spruce bark, and are considered generalist predators in the galleries of the bark beetles (Weslien 1992a). Some other species of the same genera probably have similar habits, but are less studied. Larvae are also voracious. *N. lentus* prefers open places near clearcuttings while *Q. plagiatus* is more common at closed canopy (Johansson et al. 2007). Both species seem to transmit into newly infested bark beetle galleries relatively late in summer. According to Weslien (1992a), these species were present only in the bolts that had been in the forest for at least eight weeks. *N. lentus* is present both during and after the presence of *I. typographus* larvae (Saalas 1949), which implies it to be generalist predator.

1.6.7. Elateridae – Click beetles

While feeding habits of click beetles (Elateridae) are diverse and relatively unknown, at least some of the species are proven to feed on other insects (Trougott et al. 2008). For a long time, click beetles have been known to be omnivorous, although field experiments about the subject are difficult to arrange. While many species are known as severe agricultural pests, at least genera *Athous, Melanotus, Ampedus, Prosternon* and *Danosoma* include predator or omnivore species (Saalas 1949, Trougott et al. 2008). The larvae are often encountered under bark. It is therefore assumed that these elaterid larvae at least occasionally feed on scolytid larvae. Elaterid adults are commonly encountered in pheromone traps (e.g. Valkama et al. 1997), which is to be debated whether it is due to an active lifestyle, smell of beetle carcasses or a kairomone effect.

1.6.8. Other potential Coleopteran antagonists.

Many other coleopteran families remain potential natural enemies, either by omnivorous feeding strategy or generalist predation. The impact of these less common enemies is uncertain, since their numbers are relatively low and occurrence is less frequent compared to families mentioned earlier. These are also not as recurring, but instead are mentioned inconsistently in the literature. It is most likely a few most important enemies that accumulate most of the reduction of *I. typogaphus* broods, as have been on other bark beetle species (Schroeder 1997). It also is possible that management practices impair other species, leading into overestimating the significance of these few already noted regulators. Therefore, less frequent species should be assessed case wise in order to avoid neglecting potential population regulators.

Family Zopheridae has several species mentioned to feed on different stages of immature bark beetles. Common species mentioned are *Bitoma crenata* (Fabricius, 1775) and *Aulonium ruficorne* (Olivier, 1790) (Herard and Mercadier 1996). Former had been encountered in pheromone traps during summer 2018, when flight activity of the *I. typographus* on the plots was monitored.

Salpingidae is potential family of natural enemies. At least genera *Rabdocerus* (Mulsant, 1859) (Wermelinger 2002) and *Salpingus* (Illiger, 1801) (Wegensteiner et al. 2015) have been associated to *I. typographus*. While these genera are not generally noted as significant regulators, numbers have been notably high in some studies (e.g. Wermelinger et al. 2013).

Beetle *Nemozoma elongatum* (Linnaeus, 1761) has been identified as a predator of bark beetles (Wegensteiner et al. 2015). Other trogossitid beetles are also known predators (Wegensteiner et al. 2015), although most of these known predators of bark beetles are not confirmed to be present in Finland (de Jong et al. 2014, Rassi et al. 2015).

1.6.9. Medetera and other Dipteran antagonists

Of known predatory flies of bark beetles, genus *Medetera* have proven to be the most important and numerous (Nuorteva 1956, Weslien and Regnander 1992, Herard and

Mercadier 1996, Schroeder 2007). Larvae are carnivores, although species feeding on the *I. typographus* are claimed to be rather parasitic (Dajoz 2000). Larvae are present in late summer, many species overwintering as a juvenile (Dajoz 2000, Wermelinger et al. 2012). Predatory flies have had significant effect, which is still debated. While Herard and Mercadier (1996) deducted that beetles *Rhizophagus depressus* and *Thanasimus formicarius* fed on different lifestages of prey in a complementary synergy later supplemented by parasitoids, *Medetera* was observed to have contradicting lifecycle. Flies are present when bark beetle larvae have already been infested by parasites. Competition on the same prey in the late summer means that while potential controlling effect is significant, *Medetera* may not actually accumulate to *I. typographus* brood reduction if also parasitoids are present. As *Medetera* larvae consume only one or few prey during its development, genus needs to very numerous before having a significant regulating effect (Mills 1985).

1.6.10. Pteromalidae and Braconidae

Parasitoid wasps from two major families *Pteromalidae* and *Braconidae* are common parasitoids of *I. typographus* (Schroeder 2007). Pteromalid species emerging from galleries of *I. typographus* in great numbers include *Rhopalicus tutela* (Walker, 1836), *Dinostichus eupterus* (Walker, 1836), *Tomicobia seitneri* (Ruschka, 1924) and *Roptrocerus xylophagorum* (Ratzeburg, 1844) (Weslien 1992a, Georgiev and Takov 2005, Hilszczański et al. 2007). Braconids seem to be generally less numerous (Weslien 1992a). Parasitoid wasps usually emerge relatively late in summer (Weslien 1992a, Wermelinger et al. 2012) in order to avoid shortage of hosts in case of delayed development of host species. While parasitoids are effective, these are limited to one host within its lifecycle. Their effect on the population dynamics can be seen supplementary compared to main predators emerging in early spring (Herard and Mercadier 1996).

1.7. Earlier studies on natural enemies

While earlier studies have produced reliable information, results are difficult to generalize due to vast distribution of *I. typographus* in different climatic areas. Studies of *I. typographus* have been concluded for over a century in a vast geographic area. Finland is located norther than other study sites and further in east than any other European country

where the subject has been studied. Studies on natural enemies have been conducted at least in Switzerland (e.g. Wermelinger et al. 2012), France (Warzée et al. 2006), Romania (Fora et al 2014), Poland (e.g. Hilszczański et al. 2007, Grodzki 2016), Sweden (Weslien and Schroeder 1999, Schroeder 2007, Johansson et al 2007), Italy (Faccoli 2000, Faccoli and Bernardinelli 2011), Georgia (Kereselidze 2010) and Bulgaria (Georgiev and Takov 2005, Doychev et al. 2016), as well as in Asian subspecies of *I. typographus* in Japan (e.g. Lawson et al. 1996). Studies strictly on natural enemies are scarce in Finland, concentrating mainly on the differences of fauna between managed and pristine stands (e.g. Martikainen et al. 1999).

The differences between earlier studies occur in both climatic variables and forest structure. Bivoltinism, two generations of bark beetles in one summer are more common in e.g. Poland and Switzerland than in Sweden and Finland due to greater cumulated temperature. In addition, Polish stands are more commonly mixed stands (Hilszczański et al. 2007), while Swedish are mainly mature single species spruce stands. This will generate uncertainty between results, since generalization of heterogeneous data is difficult. Earlier summaries indicate that most known predators are more likely to be generalists (Mills 1985, Kenis et al. 2004, Johansson et al. 2007, Wegensteiner et al. 2015), preying other species while population levels of the bark beetle are on the endemic level. This is also supported by the fact that, several beetles emerge before their prey, while more specialized parasitoid wasps and flies emerge usually weeks later than their prey (Wermelinger et al. 2012). In order to prevent outbreaks in commercial forests, it would be important to find out in which circumstances the predatory pressure is at its maximum. According to these earlier studies (Schlyter and Lundgren 1993, Hilszczański et al. 2007, Schroeder 2007), predatory pressure would be highest and amount of easily obtainable nutrition at minimum in managed stands. This is problematic to prove, as species that cannot prosper in managed stands may actually have great impact, which goes undetected in small natural reserves. Due to contradictions mentioned and need of alternative methods of preventing damage induced by bark beetles, more study is still required.

1.8. Damage prevention and need for the study

I. typographus colonizing new host tree can breed faster than its enemies can. Enemies colonize the same space, often with delay. This result escape in space (Schroeder 2007) and allows pest population to increase into harmful levels before controlling agents start to limit the population growth. It is shown that numbers of natural enemies of *I. typographus* increase for at least two years after initial disturbance (Wermelinger 2002). This is not simple issue, as in case studies enemy populations have occasionally grown at the same pace as *I. typographus* (Wermelinger 2013). Since facultative natural enemies could maintain their increased numbers by feeding on other bark beetles while spruce bark beetle is at endemic level (Martikainen et al. 1999), associated fauna and forest health status could affect the risk of future outbreaks. In many studies, brood reduction is cumulated by very few species (e.g. Schroeder 1997). These are usually species, which succeed at the managed conditions. It is still unclear whether these species are truly the only ones with significant reducing effect or are these the only ones that prosper in numbers high enough in managed stands to reproduce at the pace of *I. typographus*. It is suggested that natural enemies are more sensitive to different methods of management than their prey (Weslien and Schroeder 1999). Especially for the semivoltine and species overwintering in the logs, risk of being removed from the stand during sanitation loggings is high.

One important aspect has risen in recent years, as restoration and deadwood has become more acceptable in public eyes, even preferable as a mean of conservation. *I. typographus* can be therefore seen as a keystone species, of which e.g. many saproxylic species are dependent on (Müller et al. 2008). There is a slight conflict of interests between increased amount of deadwood and forest health. Since spruce bark beetle is capable of using phloem while it is fresh, both restoration projects and deadwood generated by natural disturbances may prove hazardous in short term for the remaining or neighbouring stand (Angst et al. 2012, Kärvemo et al. 2017). *I. typographus* has also potential for lowering the carbon storage (Seidl et al. 2008). Restoration by burning would be safer solution, as phloem is then dry and deteriorated (Eriksson et al. 2006). On the other hand, it is suggested that competing other bark beetle species could have antagonistic interaction with *I. typographus,* as well as support natural enemies while pest is still at endemic level. In other words, these could serve as a food source for enemies and compete for space. It

has been noted that conservation and restoration must be conducted carefully to prevent creating susceptiple conditions for pests and pathogens (Ferrell 1996). Importance and specific effects of restoration are still debated, and controversies between results still exist (Grodzki 2016).

In earlier studies, numbers of natural enemies and species have been increased in older, pristine forests (Martikainen et al. 1999, Johansson et al. 2007). This is very probable to be a cause of secondary bark beetles. For the generalist predators, deadwood might provide stable supply of secondary bark beetles (Martikainen et al. 1999), increasing the resistance at the stand level in the following years. Single groups of deadwood could therefore sustain natural enemy complex, improving resilience against future insect outbreaks. There are also results of opposite phenomenon, important species like *Thanasimus*-ant beetles being more common at managed stands (Hilszczański et al. 2007, Schroeder 2007). This is not a simple claim, as predators have been observed in increased numbers in neighbouring stands after disturbance (Wermelinger 2013). Secondary bark beetle species could also distract predators from primary pests, reducing predatory pressure for single species. This is partly supported by Schroeder's study (2007), in which the predatory pressure two years after the initial disturbance was still higher in the managed stand compared to unmanaged.

Most effective and cost-efficient preventative method seems to be removing fallen and dying trees from the stand (Niemeyer 1997). Models indicate that these sanitation cuttings and loggings performed nowadays usually reduce risk of following damage (Jönsson et al. 2012). In contrast, Stadelmann et al. (2013) noted that outbreaks cannot be totally controlled even with loggings, once epidemic phase has begun. Natural enemies are important part of this conflict, since they have impact on the pests in the areas, where sanitation loggings are not allowed due to regulations. Natural enemies can thus be used to control pests in areas, where sanitation loggings are not feasible or even borderline possible. Sanitation felling, picking single dead or dying trees from the stand may actually prove more harmful than leaving small amounts of deadwood in place. Damage caused to remaining stand by felling and logging, as well as risk of *Heterobasidion* root-rot as a follow up cause of mortality afterwards (Ferrell 1996) would require alternative control methods for insect pests.

1.9. Research objectives and hypotheses

Main objective of the current study is to observe differences in the occurrences of important natural coleopteran enemies of I. typographus in different stages of disturbance in Finnish conditions. Question is approached from the view of the forest health, in the boreal zone of Eastern Finland. If health status of the forest stand affects the natural enemy complex, management practises can increase or decrease predatory pressure that regulates the pest. Further goal is to find differences that could suggest how enemies could be integrated in to the practical forest management. This subject is quantified with trapping experiment using *I. typographus* individuals as a lure.

Research objectives are studied through three forest stand classes: (1) healthy reference forest, (2) plots with early outbreak of the spruce bark beetle with no significant earlier disturbances and (3) declined outbreak with significant amount of deadwood (accumulated by both initial storm disturbance and succeeding biotic damage).

The current study is approached through the following hypotheses:

1) **H_0** = Numbers of natural enemies are not greater in the outbreak classes compared to the healthy reference.
   H_1 = Numbers of natural enemies increase as forest health shifts from healthy to more severe infestations.

2) **H_0** = Enemy species are not affected by the health status of the stand. Conditions in the inhabited tree are more important.
   H_1 = There are enemy species which are affected by health status of the stand.

3) **H_0** = Natural enemy populations can adapt to the increased *I. typographus* population already during the first year of *I. typographus* outbreak.
   H_1 = *I. typographus* reproduces faster and outbreed its enemies. Natural enemy populations respond with delay to increased bark beetle numbers.

2. MATERIALS AND METHODS

2.1. Study area and sampling plots

A fieldwork for current study began in May 2018, and ended in October 2018. Study area was located in South-Eastern Finland, Ruokolahti municipality (Fig. 1). Long time average of the two closest weather stations for mean annual temperature is 4.0 ˚C and for precipitation 629 mm (Pirinen et al. 2012). All sampling plots were Norway spruce (*Picea abies* L. Karst.) dominated, mostly medium fertile Myrtillus type stands with occasional indicators for Oxalis-Myrtillus type in the Cajanderian classification (Cajander 1926, 1949, Hotanen et al. 2008). All plots were located on the managed forests, although plots of the declined outbreak class (Viitalampi) were located in areas, which were excluded from commercial forest management in 2011.

Variation in canopy coverage affected shrubs and ground vegetation. Most abundant moss was red-stemmed feather-moss (*Pleurozium schreberi* Mitt.), although mosses were strongly in decline on the plots of the declined outbreak class. Ground vegetation was mostly covered with blueberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idaea* L.) occasionally flourishing on drier spots. Wavy hair-grass (*Deschampsia flexuosa* L. Trin.) and oak fern *(Gymnocarpium dryopteris* L. Newman) were common on the stands with gaps in the canopy. While the dominant species was Norway spruce, a few stems of birch (*Betula pendula* Roth. and *B. pubescens* L.) and Scots pine (*Pinus sylvestris L.*) were in isolation between spruces. Rowan (*Sorbus aucuparia* L.) and aspen (*Populus tremula* L.) were sprouting on the forest floor.

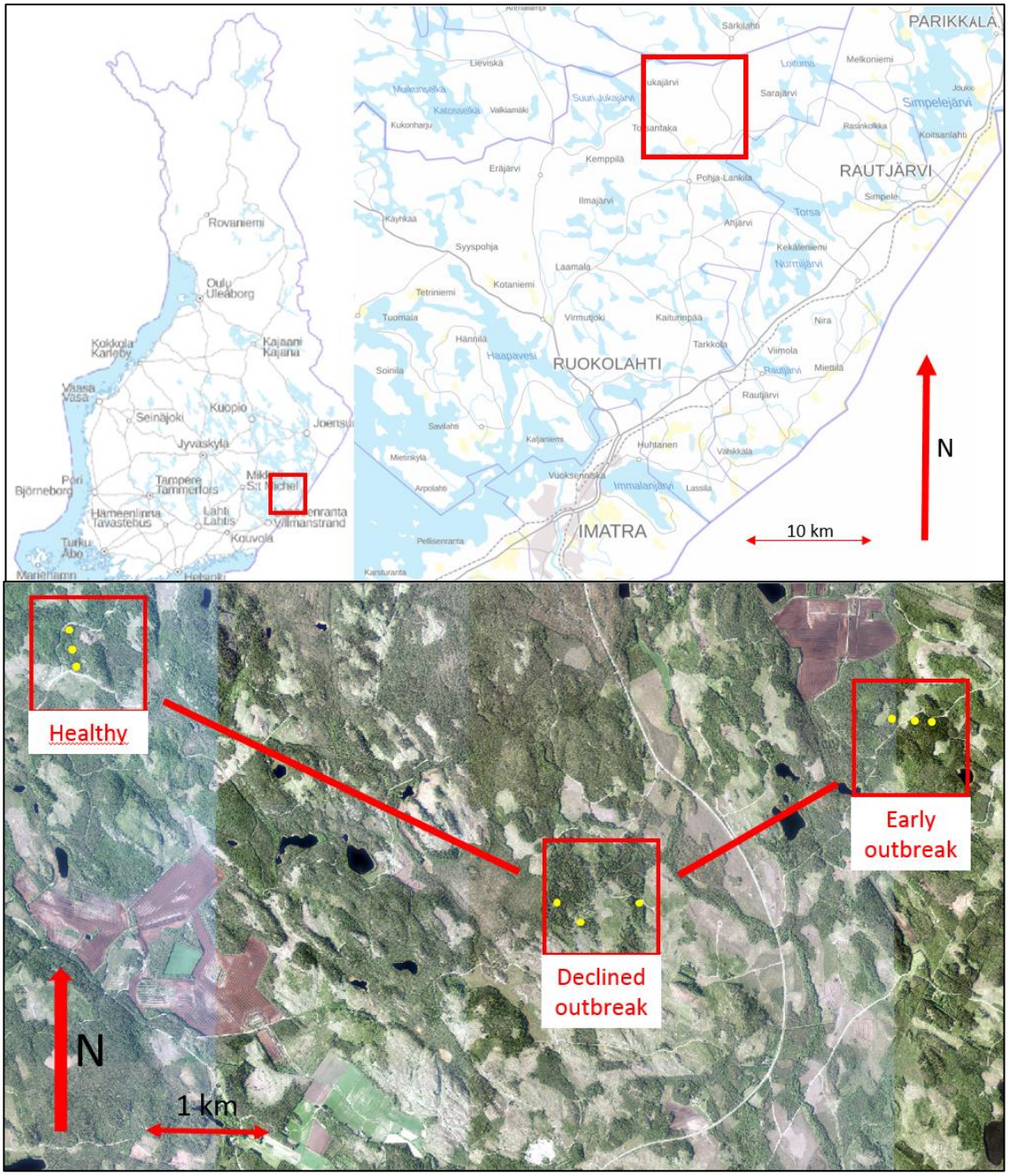

Fig. 1. Location of the Ruokolahti-municipality and the study area in the 2018. Maps and aerial image are from the Finnish national land survey 11/2019. All plots (yellow) of the same stand class were located in the same cluster. Study areas were close to one another to keep geographic influences at minimum.

Sampling plots (Table 1) were divided into three classes based on two parameters: resinous flow as a symptom of bark beetle attack and deadwood as indicator of past wind and bark beetle induced disturbances. These classes are also later referred as stand classes. All three stand classes consist of three plots, totalling nine plots. One third (n = 3) of the plots were on the healthy stands, with no visible damage in May (class later referred as the healthy). Trees did not have visible resinous flow during spring, and amount of deadwood on ten-meter radius around the center of the plot was less than one cubic meter. Population and density of the spruce bark beetle was assumed to be on the endemic level. Second third (n = 3) of plots were located in area, where outbreak was on the progradation stage, trees having resinous flow, but so far having no dead trees (class later referred as the early outbreak). In addition to resinous flow caused by bark beetles, some trees also had signs of *Heterobasidion* root-rot, implying overall weakened defences. Last third of the plots (n = 3) were located in the area where population of spruce bark beetle had already reached the epidemic level, collapsed and population had slowly started to decline towards endemic population levels (class later referred as the declined outbreak).

Table 1. Stand classes, plot numbers and coordinates (± 5 m) of a midpoint of the sampling plots in the Ruokolahti study area. Class indicates Ips typographus outbreak status of each plot. The ETRS-35FIN coordinate system was applied with the study.

Class	Plot no.	Coordinates	
		X	Y
Healthy	1	604858	6821143
	2	604815	6821281
	3	604770	6821409
Early outbreak	4	611418	6820752
	5	611601	6820712
	6	611782	6820674
Declined outbreak	7	609389	6819208
	8	608882	6819075
	9	608733	6819265

Gradation in the declined outbreak class was originally induced by abundant deadwood due to the storms. Summer storm Asta and smaller wind disturbances within next two weeks struck the area in 2010 (Viiri et al. 2011). Winter storm Tapani (referred as "Dagmar" outside of Finland) struck in 2011 (Jokinen et al. 2015). All plots of the declined class were located on the proximity of Viitalampi-conservation area (Fig. 1), since it was the only available location without sanitation loggings after the disturbance. All three plots of this class have more deadwood than Finnish regulations for forest health (Forest damages prevention act 1087/2013) would otherwise allow (>10m^3/ha in spruce dominated stands). While insect outbreak had declined on that area, single healthy trees have been infested years after the storm disturbance. These plots are comparable to less damaged classes, since stands were under management until the storms struck. Plots in the declined outbreak class (Viitalampi) are a slightly exceptional, since clear cutting had been delayed despite the stand structure being beyond optimal for harvest. The early and declined outbreak classes are later collectively referred as the outbreak classes. All plots under single stand class were located within the same cluster (Fig. 1). Different stand classes were located further away from one-another, to ensure that separate classes had no exchange of insects. Maximum distance was between the healthy and early outbreak classes 6.8 kilometres and minimum between the early and declined outbreak classes 3.0 kilometres (Fig. 1). Geographical distance between plots could not be further to ensure similar climatic and topographic conditions.

Basic stand structure was measured for each plot (Table 2). Established sampling plots were 10 meter in diameter. The amount of coarse woody debris was generalized per hectare by measuring the volume of deadwood located on the plots. As the healthy and eatly outbreak classes had no windthrown trees, amount of deadwood was insignificant. Stand structure differed slightly between plots. The plots under the healthy class were, based on the diameter, slightly younger than the two other classes. The declined outbreak -class had already lost some of its volume as windthrown trees.

Table 2. Basic stand structure of the stand classes. Number of trees (N) on a plot, diameter at 1.3m height (DBH) and height (Height) were measured for each tree with DBH≥5cm. Basal area (BA) and coarse woody debris at ground level (CWD) were generalized to square/cubic metres per hectare. Differences in stand structure were analysed with Kruskal-Wallis test. Significant (p<0.05) differences are bolded.

	Healthy	**Early outbreak**	**Declined outbreak**		
	Min - Max Mean ± s.d	Min - Max Mean ± s.d	Min - Max Mean ± s.d	Kruskal-Wallis (H)	p
N (trees/plot)	22 - 30	14 - 18	10 - 28		
	25.33 ± 3.34	16.0 ± 1.63	16.33 ± 8.26	3.29	0.193
DBH (cm)	5.0 - 33.6	14.1 - 38.4	5.6 - 46.1		
	18.06 ± 6.24	25.32 ± 5.32	22.6 ± 9.73	**32.64**	**0.000**
Height (m)	2.5 - 23.0	10.5 - 27.0	2.0 - 29.0		
	16.22 ± 5.09	20.62 ± 3.16	18.31 ± 8.22	**24.52**	**0.000**
BA (m^2/ha)	20.75 - 27.28	23.54 - 29.65	23.93 – 31.39		
	23.63 ± 3.33	26.36 ± 3.08	26.47 ± 4.26	1.69	0.430
CWD (m^3/ha)	<1	<1	380		

Furthermore, level of infestation was classified by applying infestation index approach. This index was first published by Blomqvist et al. (2018), and it measures infestation based on visual signs of attack on spruce. Infestation index was developed in Viitalampi area in 2012–2014. Parameters for index were measured during late August, once the signs of attack caused by the first generation were visible. In this index, each visual symptom is given score from one to three (symptoms of attack on tree trunk) or from one to four (symptoms on the crown) (Table 3). Three most relevant parameters for *I. typographus* – resinous flow, crown colour and defoliation – were used to evaluate the attack. This index gives individual attack score between 3 and 11 for each tree. This divides trees into three classes: no infestation (score 3-4), moderate infestation (5-7) and severe infestation (8-11). All trees were assessed and divided to these classes by the index (see Table 4 in results). This gives evidence whether the plots were correctly placed.

Table 3. Infestation index (Blomqvist et al. 2018) was applied in the current study, adopting defoliation, crown colour and resin flow as an indexed symptom. Each tree was given symptom values for indexing the infestation.

Symptom	Class	Description
Defoliation	1	0 - 25 %
	2	25 - 50 %
	3	50 - 75 %
	4	75 - 100 %
Crown colour	1	Green
	2	yellowish
	3	Reddish
	4	Grey
Resinous flow	1	0 spots
	2	1 - 30 spots
	3	>30 spots

2.2. Trapping logs

The main method of the study was to use captured, living specimens of the spruce bark beetle settled in logs of spruce to bait natural enemies in the different stand classes (Later referred as the trapping logs). All trapping log data was collected from May to October in 2018. Current method is applied from the earlier methods used by Weslien (1992a, 1994) and Weslien and Schroeder (1999).

Trapping logs required in this study were cut 13th of May, shortly after the first bark beetles flew into pheromone traps that were set to collect overwintered individuals. Trapping logs were obtained by felling two healthy trees from a private forest, within 15 kilometres distance from the Viitalampi area. Trees were cut in logs of equal height of 50 cm (± 1cm). All logs were at least 20 cm in diameter, measured from two dimensions on the narrow end, largest one being 28.9 cm. Median diameter of the logs was 23.4 cm, with arithmetic mean of 23.84 cm ± 2.69 cm. Similar earlier methods have used term bolt depicting logs of this size (e.g. Weslien and Regnander 1992, Weslien and Schroeder 1999). Each log was inspected to be uninhabited, with no sign of damage or insect entering on the bark. Logs were randomized and numbered.

Each log was first wrapped in plastic for transportation from the felling site. This was performed in order to prevent logs from drying and to keep unwanted arthropods away. In destination, each end part of the log was sealed with paraffin to keep them moist (Fig. 2). After waxing, each log was put into a metal cage covered with tight fabric to keep interfering arthropods out. There should be no insects in logs since trees were healthy and sealed during the whole process. In practice, there might have been minor number of stowaways between cracks of bark. Some nitidulid beetles (mainly *Epuraea sp*.) were encountered during felling, as well as some were encountered during waxing. While the logs cannot be entirely free of arthropods, all actions were made to keep their numbers at minimum. Keeping logs caged in all phases ensured that almost all encountered target species originate from the intended plots.

Fig. 2. Waxed log in a cage. The cage was immediately closed after the log had been treated with paraffin wax.

2.3. Settling of *I. typographus*

Ips typographus specimens where captured using pheromone traps baited with aggregation pheromone (Ipsowit[tm]). Trap model for capturing living specimens was Ecotrap[tm], manufactured by Fytofarm Ltd. (http://www.fytofarm.com/). Capturing living specimens for settling was performed in Viitalampi area, near the old, storm-disturbed plots, from 6[th] of May onwards. Nine traps were used to obtain living *I. typographus* individuals for the settling. Traps were emptied twice a day.

As living *I. typographus* individuals were collected, other species such as predators were removed from the sample. Individuals that could be identified without a microscope, *Pityogenes chalcographus* being most numerous, were also removed from this sample. Remaining sample of bark beetles was inspected to consist of physically fit *I. typographus* individuals. Threat to fitness were noted to be mainly injuries caused by the predators in traps and heat fatigue in warm days. Dead individuals, individuals that had lost limbs or inspected otherwise to be passive were excluded from settling. Final sample could still contain other *Ips* -species, or *Orthotomicus*-species of similar size. Exact numbers of beetles were not counted. Estimations of numbers of *I. typographus* were made using volume of a measuring cup (Witasek Ltd., https://www.witasek.com/), with assumption that forty individuals made one millilitre. Approximately 5000 individuals were collected for settling.

Settling began in 14[th] of May. It was done by placing trapped living individuals of *I. typographus* into surface of the caged logs. Initial number of beetles for each log before transportation to the plots was ~160 individuals. This is a small amount considering the phloem surface, but still considered large enough to initialize the colonization. Settling was supposed to act as an initial amount, later supplemented by endemic individuals from the plots. Numbers of the settled bark beetles were also kept small in order to ensure that intraspecific competition would not affect the first generation. This also means that possible sister broods had space and logs had more suitable phloem left for the insects to feed on the late summer. Having unused phloem in late summer would ensure that *I. typographus* was still present later on, giving natural enemies more time to migrate into logs. Settling was done twice a day, between 9.00 and 12.00 a.m. and from 16.00 to 19.00 p.m. When possible, each log was given equal number of beetles in captured both morning

and evening, in order to remove variation between fitness of individuals, which were perhaps suffering from the cold in at night or heat fatigue during day. Thirty percent of the settled individuals were collected before noon, while seventy percent later during the day. This means that equal amount was not possible. Initial number of beetles in each log was reached and settling considered successful in 27th of May.

2.4. Plot setup and pheromone trapping

Once the settling was complete, trapping logs were taken to the plots and uncaged. Three settled logs were placed on the perimeter of each plot, forming a triangle around the centre of the plot (Fig. 3a). In contrast to several other studies (e.g. Hilszczański et al. 2007, Schroeder 2007), trapping logs were completely unbaited. Settled living individuals of *I. typographus* were supposed to act as a bait themselves for natural enemies. Settled logs were placed horizontally with one edge elevated from the ground (Fig. 3b). Elevation was made using local deadwood. This was done in order to mimic fresh deadwood, which is rarely in contact with the soil. This also prevented ants (mainly *Myrmica sp.*) from making nests underneath the logs.

For each log, a pheromone trap was placed to monitor population level of I. typographus. Pheromone product used was IT-ecoluretm (http://www.fytofarm.com/). Trap type was the same Ecotraptm model, which was used to collect I. typographus individuals for settling. Due to the nature of the traps, these were located to the nearest opening instead of measured distance. Otherwise traps could have baited I. typographus to attack nearby trees. Pheromone traps were placed in 25th of May. Logs were placed when the settling was ready, in 31st of May. Pheromone traps were emptied once a week to monitor the I. typographus population level until the last week of August. Logs were untouched across the summer. In total, each of nine plots had three logs and pheromone traps, totalling twenty-seven of each.

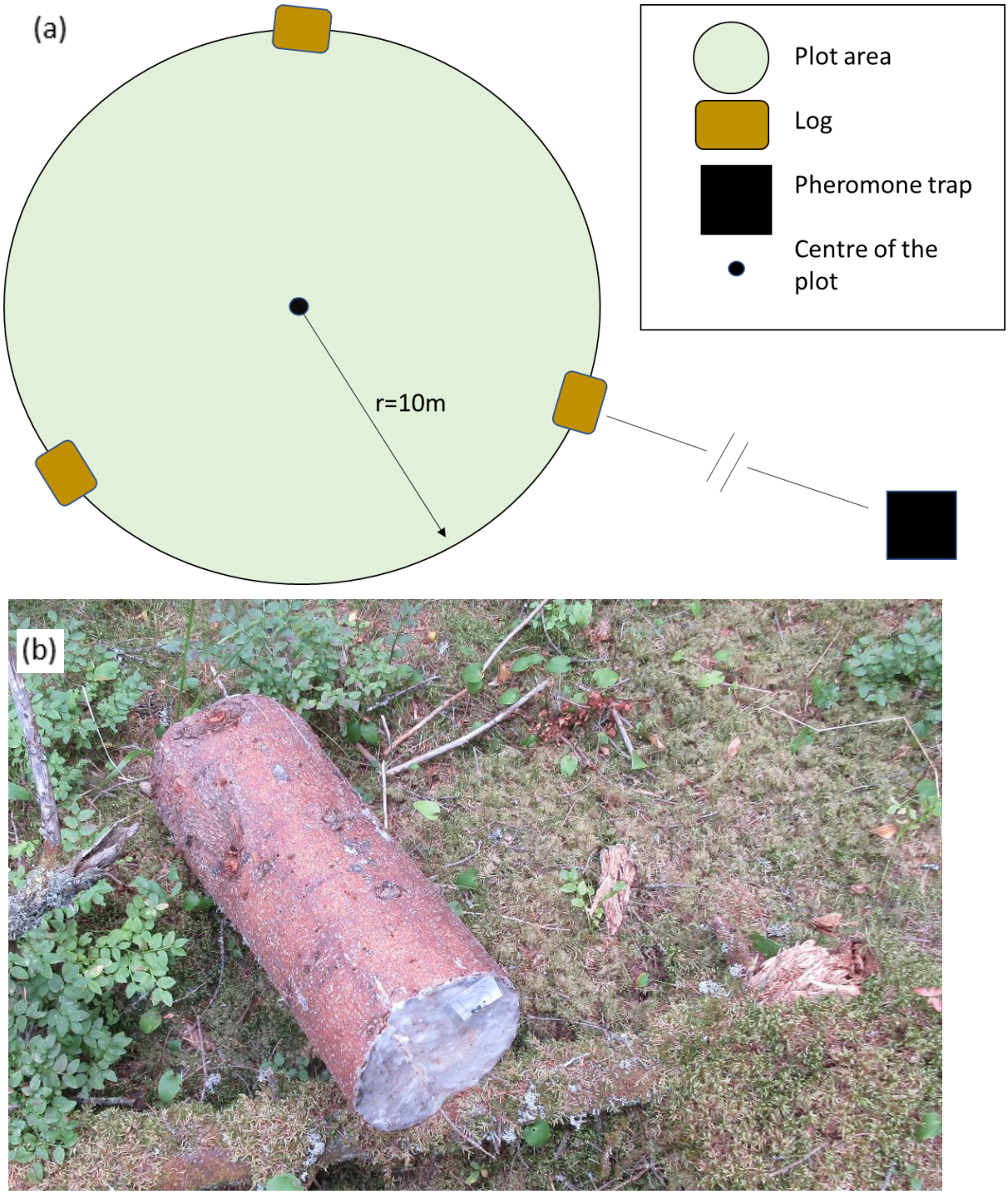

Fig. 3a and 3b. Experimental setup of a sample plot. Settled logs formed a triangle on the perimeter (a). Pheromone traps, requiring more open space, were founded further from the plot, to the first opening in the canopy. Logs (b) were placed horizontally with one edge elevated. Nine plots with a sum of 27 logs were established.

2.5. Field sampling of logs

Re-sealing trapping logs was scheduled to allow targeted predatory species to have enough time to migrate into logs, but *I. typographus* was still assumed to be active in the logs. In the first week of August, for the first time after the sister brood started to emerge in the pheromone traps, numbers of trapped individuals in all twenty-seven traps fell althogether under thousand individuals (less than forty individual on average in each trap). As the swarming of the first generation of beetles and sister brood decreased greatly in numbers, trapping logs were collected from plots. Starting from 13th of August, logs were sealed and transported from the plots before the insects inside could mature and emerge. While some enemies active in early spring may had already matured, most were suggested still to be inside the logs. Potential sister brood or second generation were also expected to still be as a larva under the bark. Metal ring was attached to the log and used to hang it. Logs were then covered with a simple fabric-covered metal net with funnel-like bottom (Fig. 4) (compare to Weslien 1992a, Weslien and Schroeder 1999). Jars of water and salt were attached to the bottom of these cages, collecting and preserving the emerging insects. Due to the prolonged warmth in autumn 2018, emerging insects were collected from cages until 27th of October, when average temperature of the day went permanently below zero degree Celsius. Cages were then sealed for the winter. Caged logs were debarked in the following summer 8th of June 2019.

All emerged insects were preserved in 70% ethanol. Collected insects of each log were identified in the laboratory to the appropriate state. For targeted species, Scolytinae and coleopteran natural enemies, species-level was intended. Other coleopteran species were identified to at least a family-level. Most of the coleopteran natural enemies were still left family or genus level, since most of the individuals were at larval stage. Other insects were inspected depending their importance and possibilities of identification. While larvae of predatory and parasite hymenopteran and dipteran families were numerous and would probably prove significant enemies, their identification were not possible in the extent of this study. Other arthropods were excluded. Most numerous of excluded arthropods were mites and springtails.

Fig. 4. A simple funnel trap setup collecting emerged insects was applied with the current study. Jar was filled by water, salt and soap. Setup was under roof to protect it from the weight of the snow.

Beetles were mainly identified by literature and comparing to scientific collections of the university. Identification was made using taxonomy provided by the Finnish museum of natural history (LUOMUS) in provincial listing of Finnish Coleoptera (Rassi et al. 2015). In addition, Fauna Europaea (de Jong et al. 2014) was inspected to see if a scientific name had contradicting synonyms. Classification between associate, antagonist and predator were made using earlier studies (e.g. Weslien 1992a, Kenis et al. 2004 and Wegensteiner et al. 2015). Contradicting classifications, if any, are mentioned in introduction.

2.6. Statistical analyses

Statistical analyses comprise of correlation analyses and analyses of variance (ANOVA). To compensate differences between individual logs and the success of the settling, statistics for each plot were later calculated using sum of three logs. Analyses of variance were used to prove the differences between insect occurrences between stand classes, in both pheromone trapping and trapping logs. ANOVA is a statistical linear model, which requires parametric data (Ranta et al. 1989). Non-linear test were used for the genera which did not achieve normality. All tests were made using IBM SPSS-software (version 24.0.). Used method was determined by the tests of normality, indicated by Shapiro-Wilk test:

$$W = \frac{(\sum_{i=1}^{n} a_i x_{(i)})^2}{\sum_{i=1}^{n} (x_i - \bar{x})^2} \quad (1)$$

Where $x_{(i)}$ is the smallest value of the sample, a_i is coefficient and $\bar{x}$ arithmetic mean of the sample.

I. typographus in the pheromone trapping followed the normality assumption, and parametric tests (ANOVA) were used. Sums and trap averages were also calculated for pheromone trap catch of each stand class. When insects emerging from the trapping logs were observed, only *I. typographus* followed the normal distribution. Data transformation was therefore attempted to achieve normality for the enemy species. Logit-transformation was applied, as it did not require proportial data. It has also been shown that commonly in ecology used arcsine-transformation is considered redundant (Warton and Hui 2011). Both transformations were nevertheless performed. These worked well with species emerging in large numbers. Less numerous ($n < 100$) but potentially important species did not achieve normality. Therefore, all of the statistical analyses of insects emerging from the trapping logs were carried out using the Kruskal-Wallis non-parametric tests. In addition to the species which emerged before winter, cerambycid *Rhagium inquisitor* larvae encountered during debarking were analysed with the same tests. Since data does not follow normal distribution, Spearman correlation was applied in correlation analyses:

$$r_s = 1 - \frac{6 \sum d_i^2}{(n^2-1)n} \quad (2)$$

Where d_i is difference between two observed ranks and n is a number of observations.

As a non-parametric test, Kruskal-Wallis rank sum test (one-way ANOVA on ranks) was used to determinate whether there were significant differences in numbers of natural enemies and associates among different stand classes:

$$H = \frac{12}{N(N+1)} \sum_{i=1}^{k} \frac{R_i^2}{n_i} - 3(N+1) \quad (3)$$

Where N is total number of observations, k is number of independent samples and R_i is sum of ranks (Ranta et al. 1989).

The level of significance used was 0.05. Dunn's test (with Bonferroni's correction) was used as a post hoc to determinate which stand classes were potentially more suitable for certain enemy groups. Only species with at least 10 individuals were analysed, since Kruskal-Wallis test will not show reliable results with sample size much smaller than that. Friedman's test was also attempted in addition to correlation analyses to inspect relation of *I. typographus* in comparison to all natural enemies. The test was used, as it is analysis of variance that can test related samples (species in current study) in a similar manner as correlation analyses. In comparison, Kruskal-Wallis requires nominal class (stand class in the current study). Finally, correlation analyses and Kruskal-Wallis ranked ANOVA were also applied to indicate whether different sources of error (e.g. log diameter) differed between stand classes.

3. RESULTS

3.1. Monitoring bark beetle activity and state of infestation on the plots

First bark beetles were encountered 8th of May, only a few days after the pheromone traps were established. *I. typographus* mass flight began after daily temperature rose above the flight threshold in 12th of May. Pheromone trap catch of the early outbreak class differed from the healthy and declined outbreak classes (Fig. 5a). Emergence of overwintered adults and re-emergence after oviposition showed continuous activity on all stand classes until mid-June (Fig. 5b). First generation showed increased numbers after mid-July, after which both re-emerged and newly matured first generation started swarming. First generation of *I. typographus* in the early outbreak class was considerably larger compared to other classes. Overall sums of trapped individuals for each stand class did not differ in statistical tests, although the first generation emerging in the early outbreak class in mid July (19th of July) was significantly more numerous compared to other classes during that time period ($F = 6.145$, $df = 2$, $p = 0.007$). Daily risk limit of 300 individuals per trap (Niemeyer 1992) was probably encountered in all forest classes during initial swarming between 31st of May and 7th of June, and during the re-mergence in 21st of June. This was not confirmed, as traps were emptied on the weekly basis. Occurrences of this magnitude continued only for a few days. Only the early outbreak class had flight of this magnitude during the first generation emergence in the mid-July.

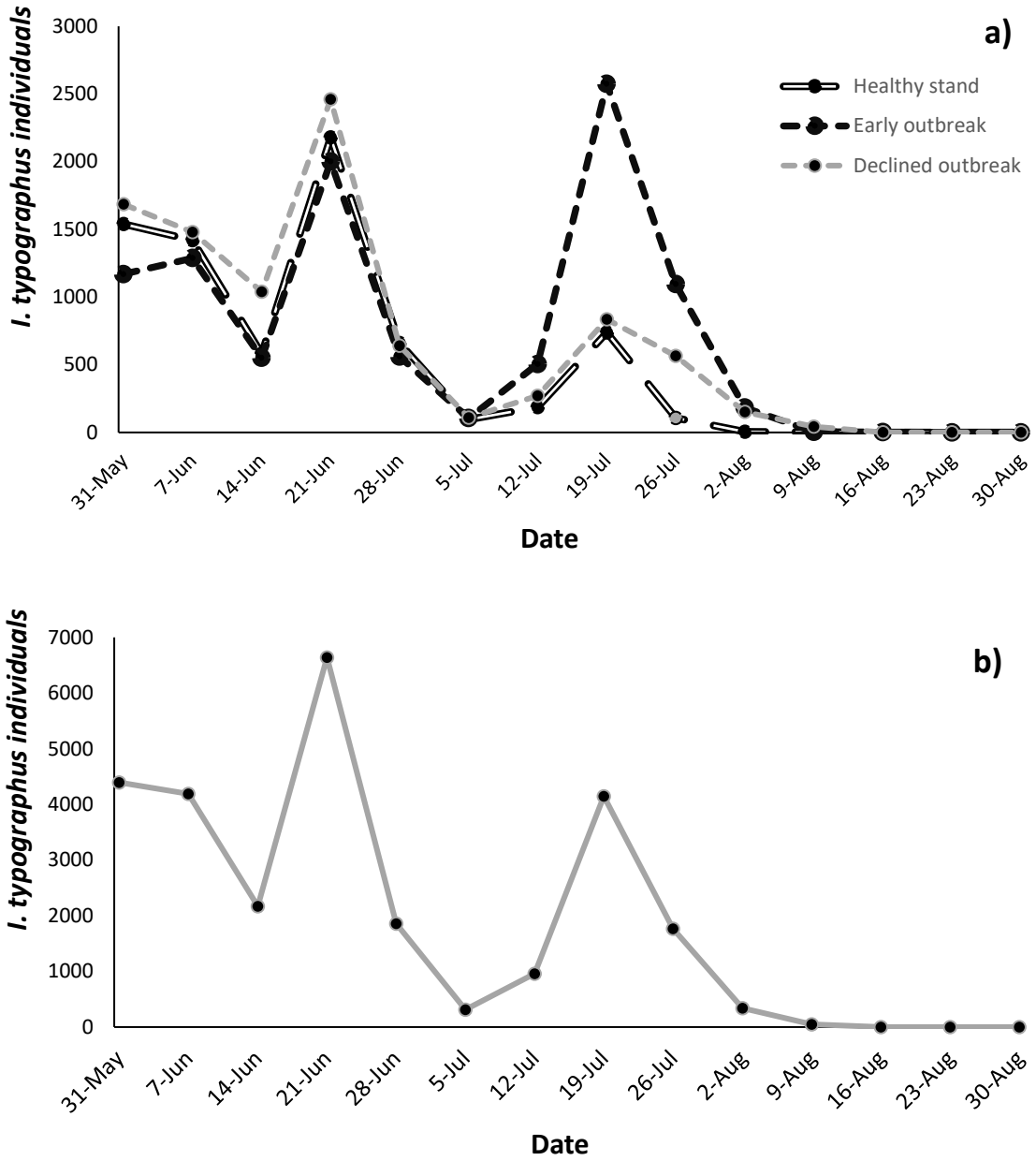

Fig. 5a-b. Flight activity of I. typographus on the plots. Results of a trap catch on the healthy stand, the early outbreak, the declined outbreak (a) and a total trap catch (b) of the species are shown. Graph a) is a result of a nine pheromone traps in each, and b) is the sum of all 27 traps. Numbers represent estimated individuals based on volumetric sample of the catch.

The infestation index implied that plots were correctly chosen (Table 4). The number of non-infested trees decrease from the healthy stand towards the declined outbreak. Moderately infested trees peaked at the early outbreak class, but greater proportion was already dead or severely infested at the declined outbreak class. Few small diameter trees were dead on the healthy stands, showing a small proportion of severe infestation.

Table 4. Trees in stand classes (n = 173) for each infestation class. Infestation index and proportion of trees in each class are presented.

	Healthy	Early outbreak	Declined outbreak
No infestation (3-4)	71.1 %	60.4 %	38.8 %
N	54	29	19
Moderate infestation (5-7)	25.0 %	39.6 %	10.20 %
N	19	19	5
Severe infestation (8-11)	3.9 %	0.0 %	51.0 %
N	3	0	25

I. typographus catch varied from ~ 2090 to 4060 individuals per group of three traps in each plot (Table 5). Trap catches of the individual traps varied greatly. While the healthy class had the least individuals, this difference was not statistically significant ($F = 0.644$, $df = 2$, $p = 0.534$).

Table 5. Total pheromone catch of I. typographus for each plot and stand class. Sum (N) is the caught spruce bark beetle individuals in three pheromone traps for each plot and class total is sum of nine traps. Averages of the single trap are presented for each plot (± s.d.).

Class	Plot no	N (individuals)	Trap average ± s.d.
Healthy	1	2097	699 ± 123.6
	2	2152	717.3 ± 166.6
	3	3263	1087.7 ± 241.4
	Class total	7512	834.7 ± 256.6
Early outbreak	4	4063	1354.3 ± 438.3
	5	3428	1142.7 ± 188.0
	6	2545	848.3 ± 23.5
	Class total	10036	1115.1 ± 345.1
Declined outbreak	7	2642	880.7 ± 240.1
	8	2606	868.7 ± 156.8
	9	4036	1345.3 ± 92.2
	Class total	9284	1031.6 ± 282.0

3.2. Bark beetles emerging from the logs

Total number of beetle individuals emerging from the logs (n_{total}) was 8514. Most of the beetles from the logs (n_{scol}=6751) were bark beetles (subfamily Scolytinae). More *I. typographus* individuals colonized logs after settling, and the species represents 72 percent of the Scolytinae and 57 percent of all emerged beetles. The three most abundant bark beetle species *Ips typographus* (72%, n = 4875), *Dryocoetes autographus* (18%, n = 1223) and genus *Crypturgus* (8%, n = 509) (Fig 6.) consisted of 98 percent of all scolytids. Nine other species of Scolytinae were encountered, totalling the remaining two percent (listed in Appendix 1). Many other secondary bark beetle species emerged almost exclusively from the declined outbreak -class with already diminished numbers of the spruce bark beetle, e.g. species *Hylastes cunicularius* and *Ips duplicatus*. Althogether 65 percent (n = 74) of these secondary bark beetle species were encountered on the plots of declined outbreak.

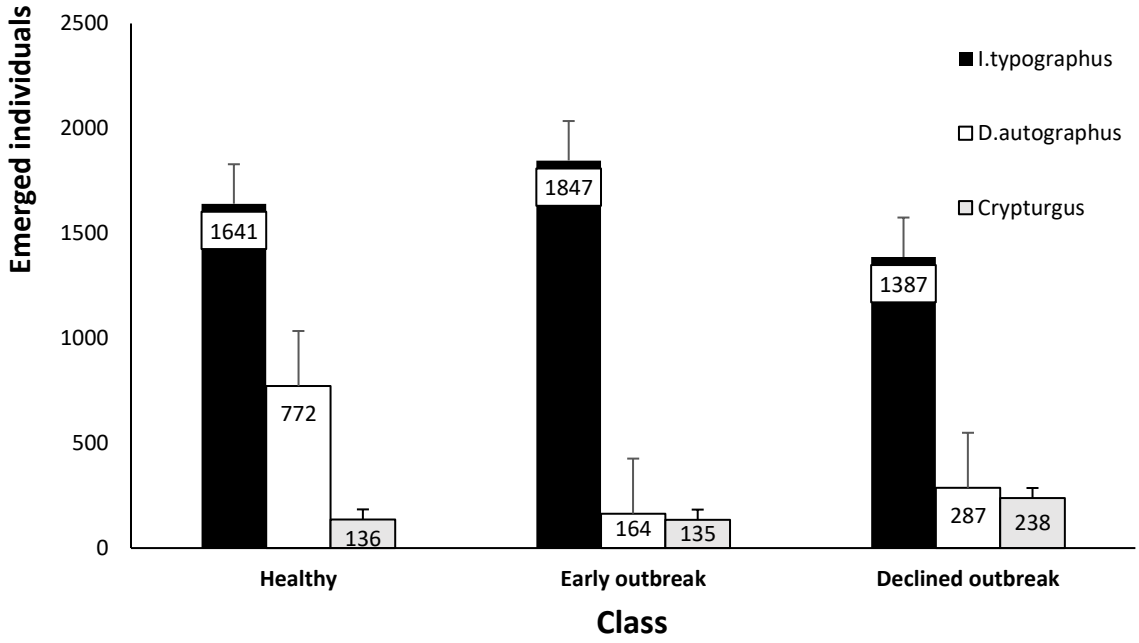

Fig 6. Emerged common bark beetles by the stand class (+s.d.). Three major species were Ips typographus, Dryocoetes autographus and genus Crypturgus, comprising of 98 percent of all bark beetles.

Dryocoetes autographus preferred the healthy class (Chi square = 12.036, df = 2, p = 0.002), in which it was almost three times as numerous as in the declined outbreak, or almost five times as numerous as in the early outbreak class. The species had low negative correlation with *I. typographus,* but it was not statistically significant. *Crypturgus* spp. emerged in all trapping logs, failing to show any trend despite being slightly more common at the declined outbreak. The species had correlation with *I. typographus* (r_s = 0.462, n = 27, p = 0.015).

3.3. Natural enemies emerging from the logs

Natural enemies emerging from the logs consisted of six coleopteran families. In total, 15 coleopteran species of the taxonomic groups mentioned in literature to prey on *I. typographus* emerged from the trapping logs (listed on the Appendix 1). There were nine genera of enemies that emerged as an adult. *Thanasimus formicarius, Glischrochilus sp.* and four species of elaterid beetles were encountered only as larvae. In addition to these, other species encountered were less important based on the literature in the context of *I. typographus* and disturbance dynamics. All the species emerging in significant numbers were analysed (Table 6, Fig. 8). Average numbers of individuals for trapping logs for each class are presented in the Figure 8. This excluded predatory species *Platysoma angustatum* (n = 2) and *Glischrochilus sp*. (n = 7, only larvae) emerging in too low numbers to analyse.

Natural enemies emerged in the greatest numbers from the logs of healthy class, early outbreak being only marginally less numerous (Fig. 7). The declined outbreak-class had least beetles in overall, both natural enemies and bark beetles. Natural enemy adults had relatively strong correlation with emerged *I. typographus* (r_s = 0.508, n = 27, p = 0.007), although total number of all enemy life stages scored higher correlation with the sum of all emerged beetles (r_s = 0.739, n = 27, p = 0.000).

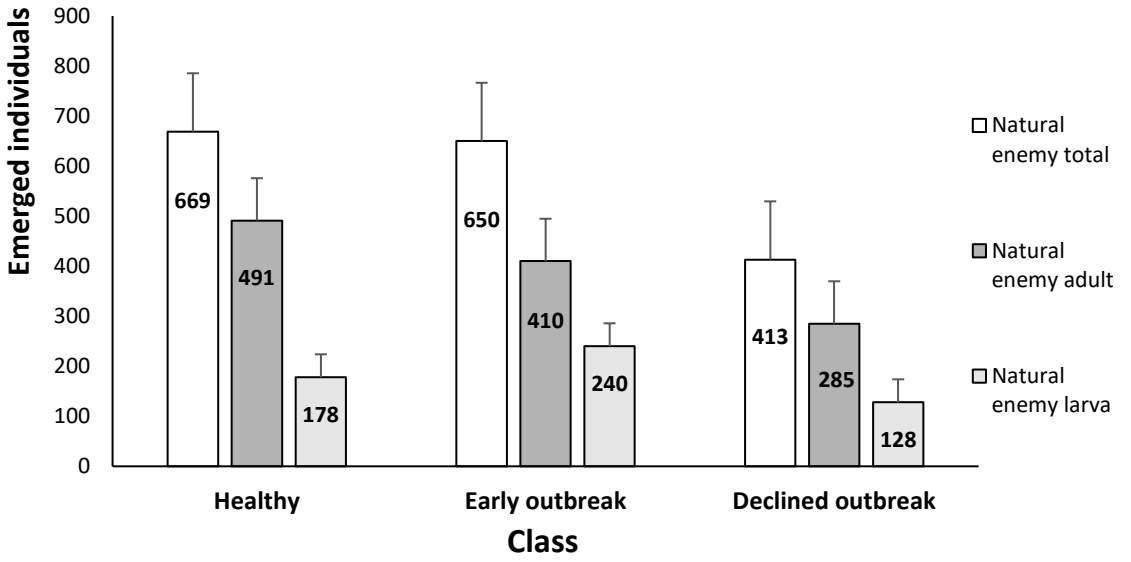

Fig. 7. Total numbers of natural enemies emerging from the trapping logs (+s.d.). Total number of enemies was very similar in the healthy and early outbreak classes. While the declined outbreak class had less individuals, statistical tests did not imply significant difference to other two classes.

Correlations for each individual enemy group are presented in the appendix 2. *Ips typographus* and total numbers of enemies did not occur in similar patterns (Chi square = 22.154, df = 1, p = 0.000). Natural enemies as a single group had no preference for stand class (Chi square = 3.363, df = 2, p = 0.186). Kruskal-Wallis test pointed out three genera with statistically proven preference on the stand class (Table 6). In addition, genus *Quedius* had near significant preference. Excluding the already mentioned taxonomic groups and bark beetles, no other beetle species or families emerged in sufficient numbers for analyses.

Table 6. Occurrence of the most frequent coleopteran enemies. Numbers are accumulated from nine logs in every stand class. Enemies were encountered both adult (A) and larval (L) stages. Kruskal-Wallis test was applied. Results significant in the 0.05-level are bolded (º = near significant).

Predator	Healthy	Early outbreak	Declined outbreak	Kruskal-Wallis H	p
Plegaderus vulneratus [AL]	41	179	51	**6.415**	**0.040**
Phloeonomus spp [A(L)]	421	203	200	**6.362**	**0.042**
Quedius plagiatus [A(L)]	21	4	3	5.455	0.065º
Nudobius lentus [A(L)]	7	2	2	1.582	0.453
Thanasimus formicarius [L]	12	0	5	**6.413**	**0.040**
Elateridae spp. [L]	7	2	7	1.371	0.504
Epuraea spp [AL]	15	15	23	0.171	0.918
Rhizophagus spp [AL]	7	14	7	1.09	0.580

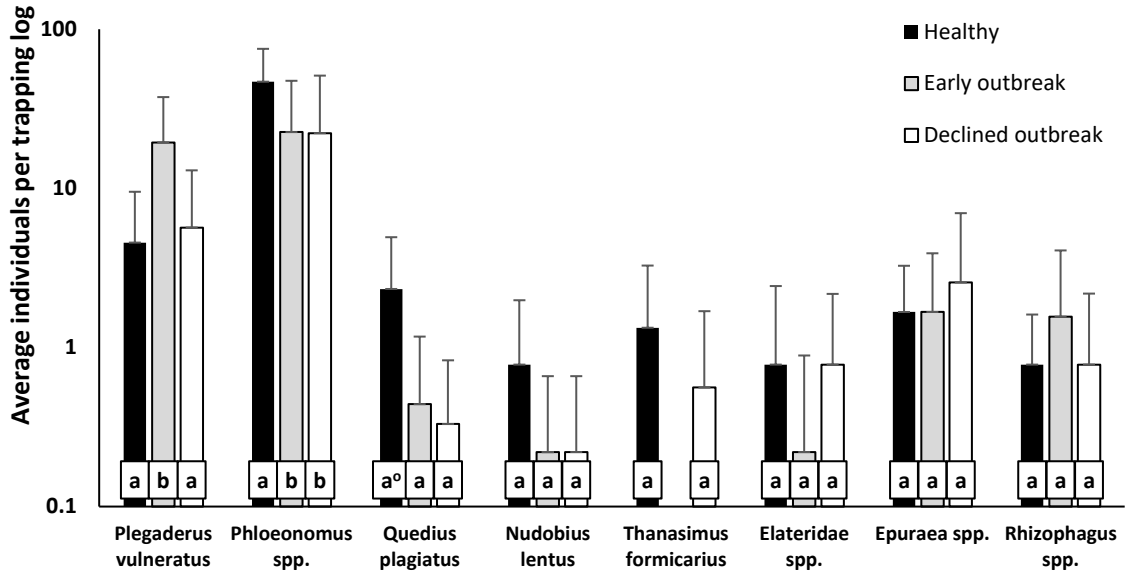

Fig. 8. Average individuals (+s.d.) per trapping log for each stand classes. Only seven most important genera and one family were inspected. Scale is logarithmic. Differences in occurrences are indicated by letter and are based on the Kruskal-Wallis test at 0.05-level of significance.

Most excluded beetles belonged to the families' Latridiidae, Cerylonidae and Ptiliidae. The only species absent in emergence traps but present next spring in logs during debarking was larvae of the cerambycid beetle *Rhagium inquisitor* (n = 62). While this potential competitor was more common at outbreak classes (Appendix 3), difference was not proven statistically significant (Chi square = 2.448, df = 2, p = 0.294). This was most likely due to fact, that larvae of the species were very unevenly distributed among trapping logs (i.e. logs had either none or plenty).

In addition to coleopteran predators, two families of parasitoid wasps were identified, almost all individuals belonging to Pteromalidae. As Kruskal-Wallis test was applied, tests did not indicate any differences in the occurrences of the pteromalid wasps between the three stand classes. The family was found most numerous at the healthy class (Appendix 4). Identified species were *Rhopalicus tutela* and *Roptrocerus xylophagorum*. Unknown dipteran larvae were numerous, but were left without analyses due to most being unidentified, which means that predatory were not excluded from the other feeding strategies. Predatory heteropteran *Scoloposcelis pulchella* emerged in too small numbers to analyse (n = 3). While overwintered insects were not analysed for the study, it was clear after debarking that most of the insects had abandoned galleries before winter.

In addition to absolute numbers, antagonist/spruce bark beetle ratio (Table 7) was counted. Two other bark beetle species emerged in large numbers, and these were examined as alternative prey. Relation of each individual genus to *I. typographus* is represented in Table 8. Logs were debarked at 8th of June 2019. Emerged insects were not identified for this study, but small volume of captured insects in the spring implied that most insects matured and abandoned logs before the winter. Many insects left logs while still being at larval stage. This is either accidental or insects abandoned logs for overwintering at the ground level.

Table 7. Emerged bark beetles per predator (prey/predator ratio, only adult natural enemies on parenthesis). Table assumes that generalist predators also prey on other bark beetles.

Stand class	*I. typographus*	*Dryocoetes sp.*	*Crypturgus sp.*	*Scol.other*	*Scolytinae, all*
			/Natural enemy		
Healthy	2.46 (3.34)	1.16 (1.58)	0.20 (0.28)	0.02 (0.02)	3.84 (5.22)
Early outbreak	2.84 (4.50)	0.25 (0.40)	0.21 (0.33)	0.02 (0.03)	3.32 (5.26)
Declined outbreak	3.36 (4.87)	0.69 (1.01)	0.58 (0.84)	0.12 (0.17)	4.75 (6.88)

Table 8. Predator/prey ratio for each genus (per hundred emerged I. typographus individuals). Ratio is displayed, because the healthy, early outbreak and declined outbreak classes supported different total numbers of beetles (n = 3270/2817/2427, respectively).

Antagonist genus	**Individuals/100 *I. typographus***			**Frequency**
	Healthy	**Early outbreak**	**Declined outbreak**	
Phloeonomus spp.	25.66	10.99	14.42	824
Quedius sp.	1.28	0.22	0.22	28
Nudobius sp.	0.43	0.05	0.14	10
Staph.other	0.79	1.3	1.59	28
Plegaderus sp.	2.5	9.47	3.68	271
Epuraea spp.	0.91	0.81	1.66	53
Rhizophagus spp.	0.43	0.76	0.5	28
Thanasimus sp.	0.73	0	0.36	17
Elateridae spp.	0.43	0.11	0.5	16

3.4. Coleopteran enemies – species

Species from now on are represent in the order of importance in the current study: Better-known predators before families with less certain antagonistic interaction with *I. typographus*.

3.4.1. Thanasimus spp. - Ant beetles

Kruskal-Wallis test showed statistically significant difference (Chi square = 7.278, df = 2, p = 0.035) in *Thanasimus formicarius* numbers between the healthy and early outbreak classes, of latter genus was completely absent (Fig. 9). Overall numbers were not sufficient (n = 17) to show reliable differences between different stand classes. Despite few individuals, species was more common in the healthy class compared to the declined outbreak, although this difference was not statistically proven. Despite the fact that results of this very small sample were statistically significant, generalized conclusions from this study should be made in caution.

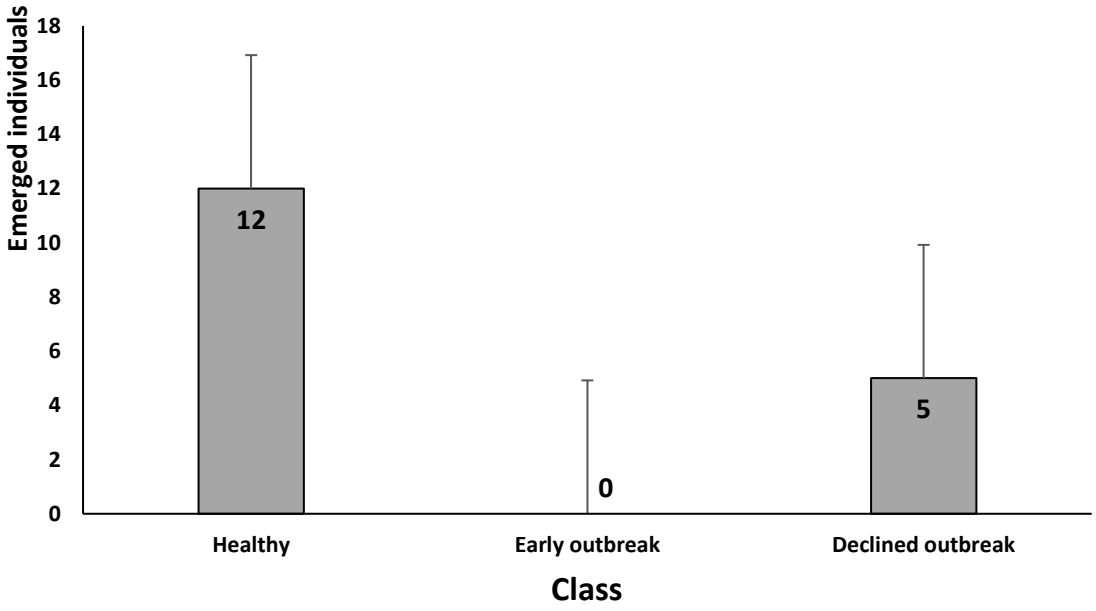

Fig. 9. Numbers of emerged T. formicarius larvae (+s.d.). No adults emerged due to long lifespan. Difference between the healthy and early outbreak classes proved significant at the 0.05-level by Kruskal-Wallis test.

Larvae abandoned logs immature instead of pupating. This was later confirmed by debarking the logs, during which the single larva encountered had not yet pupated. This means that only one larva of the eighteen overwintered in the logs. Correlation analyses showed that ant beetles occur in similar patterns like other medium-to-large predators with slower lifecycle, like *Quedius plagiatus* (r_s = 0.529, n = 27, p = 0.005) and elaterid beetles (r_s = 0.409, n = 27, p = 0.034). Significant correlation was also between ant beetles and scolytid *D. autographus* (r_s = 0.404, n = 27, p = 0.036).

3.4.2. Histeridae – histerid/clown beetles

Only two species of Histeridae emerged. Two individuals of *Platysoma angustatum* emerged from the logs in the healthy class. More numerous was the *Plegaderus vulneratus*, which was the most common single predatory species to emerge from the trapping logs (n = 271). Only staphylinid beetles of genus *Phloeonomus* were more numerous. Most of this species were encountered as an adult, only four larvae emerging in the early outbreak class. Species was significantly more numerous on the early outbreak class compared to others (Fig. 10). The occurrences of the species correlated with the *Epuraea* (r_s = 0.465, n = 27, p = 0.015).

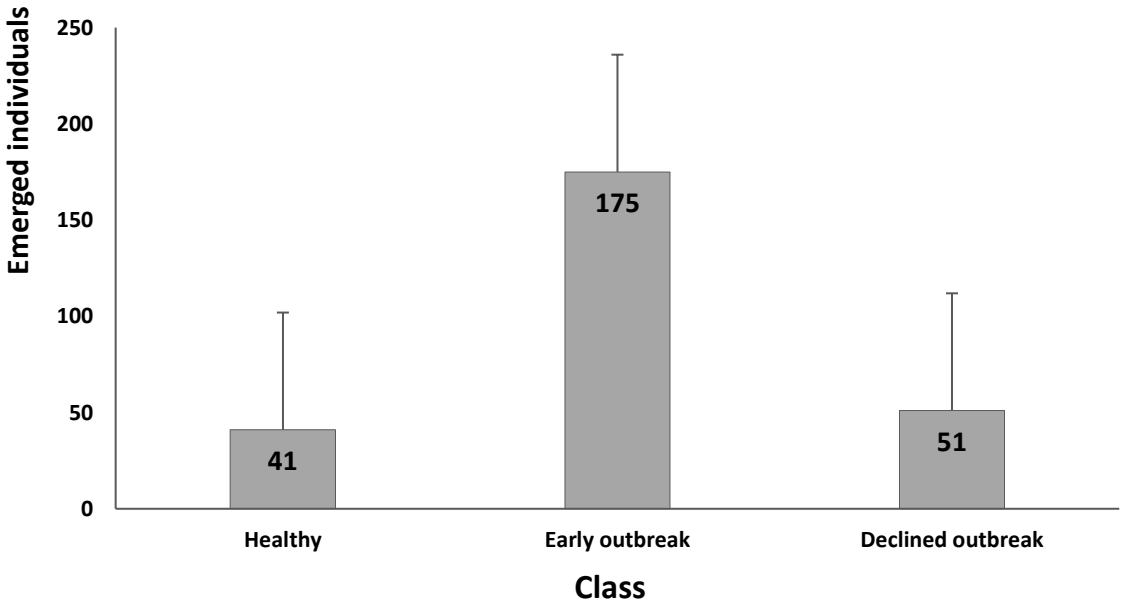

Fig. 10. Numbers of emerged P. vulneratus (+s.d.). The results of the early outbreak showed significant differences compared to other stand classes (Chi square = 6.415, df = 2, p = 0.04). Kruskal-Wallis test. Results were significant at the 0.05-level.

3.4.3. Nitidulidae – Sap beetles

Sap beetles emerged mainly as a larva from all stand classes. *Epuraea spp.* were only nitidulid genus emerging as adult, as well as the most numerous (n_{total} = 53). Therefore, it was the only genus in this family to have any correlation and significance. At least two other genera of nitidulid larva emerged from the logs. Without reliable reference at hand, there were no certainty whether these other nitidulids would belong to other predatory genera (*Glischrochilus* or *Pityophagus*). As numbers were small (n = 7) these larvae were excluded from analyses.

Distribution of all life stages were equal on the plots of healthy and early outbreak classes (n = 15), but higher on the declined outbreak (n = 23)(Fig. 11.). All of the few adult *Epuraea* (n = 4) emerged from the logs of declined outbreak. Kruskal-Wallis -test strongly showed that genus had no stand class preference (Chi square = 0.171, df = 2, p = 0.918). As predator-prey ratio between *Epuraea* and *I. typographus* was approximately double in the declined outbreak compared to other classes, genus may still have some preference.

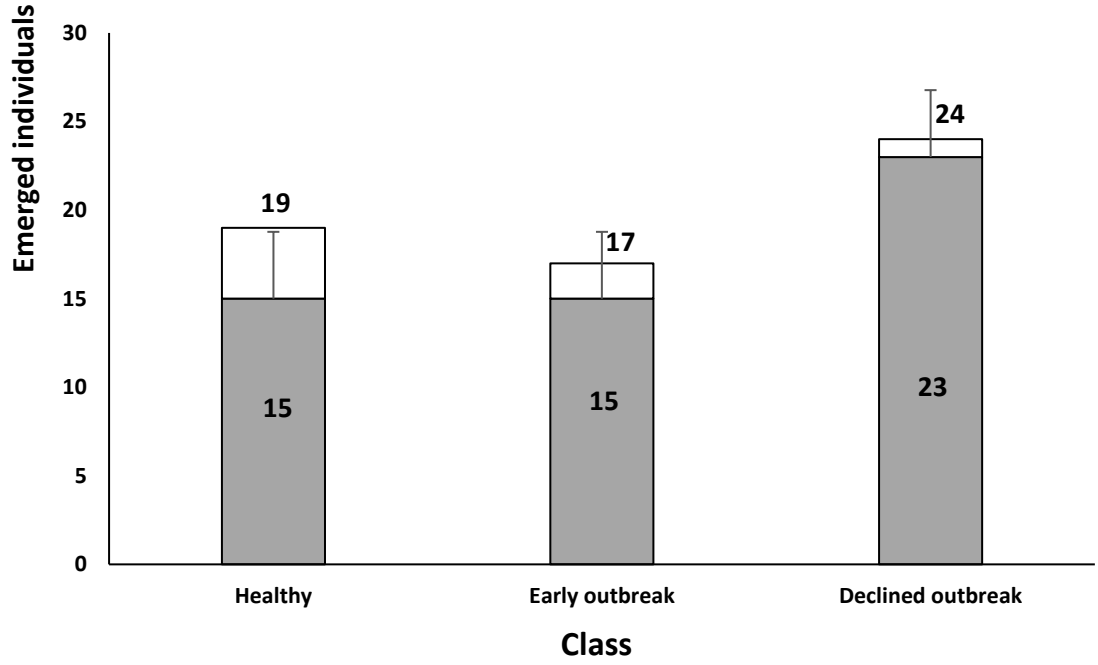

Fig. 11. Occurrence of Epuraea spp. (Grey, +s.d.) and all Nitidulidae combined (white). Kruskal-Wallis test did not find significant differences at 0.05-level.

3.4.4. Rhizophagus spp. – Root-eating beetles

Most *Rhizophagus* individuals emerged from the early outbreak class (Fig. 12), both larvae and adults.

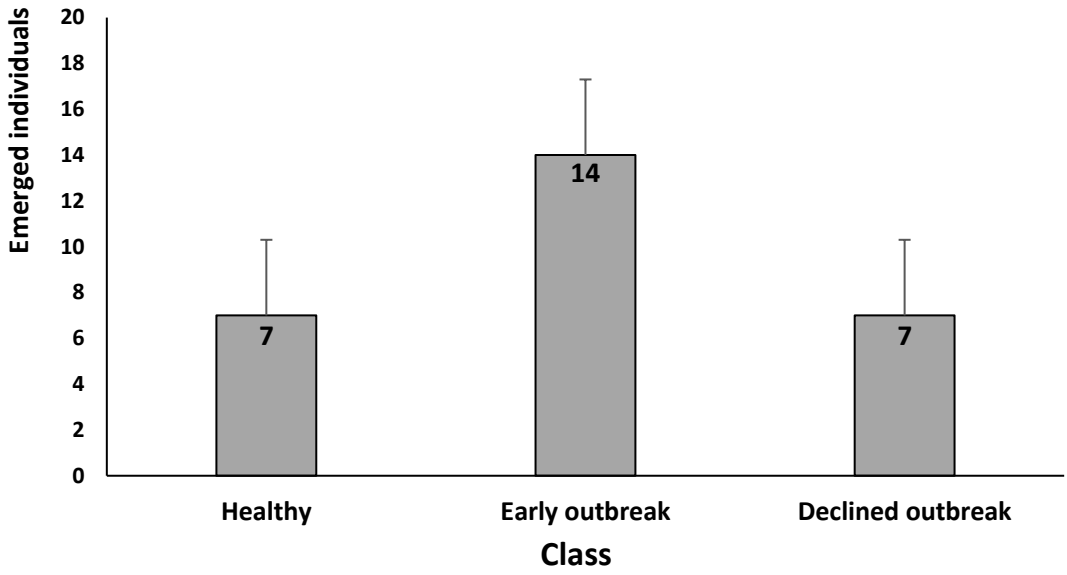

Fig. 12. Emerged Rhizophagus individuals. Kruskal-Wallis test did not find significant differences at 0.05-level even as the early outbreak had double the individuals compared to other classes (Chi square = 1.090, df = 2, p = 0.580).

While numbers were borderline sufficient to show differences (n_{total} = 28, n_{adult} = 15, n_{larva} = 13), occurrences of the genus varied greatly between individual logs within stand classes. This meant that tests failed to show statistically significant differences between stand classes, even as half of the *Rhizophagus spp.* individuals emerged from the early outbreak. The only species encountered was *R. dispar*. Species of the larvae were unknown.

3.4.5. Staphylinidae – Rove beetles

Family Staphylinidae was diverse and abundant in all logs. Excluding the bark beetles, family had most specimens (n = 1348). It was impossible to identify larvae other than late instars of larger species, or even all adults in the extent of this study. Analyses concentrated on the most important identified blocks: small abundant species *Phloeonomus* spp. and the subfamily Aleocharinae, as well as large predatory species *Quedius plagiatus* and *Nudobius lentus*.

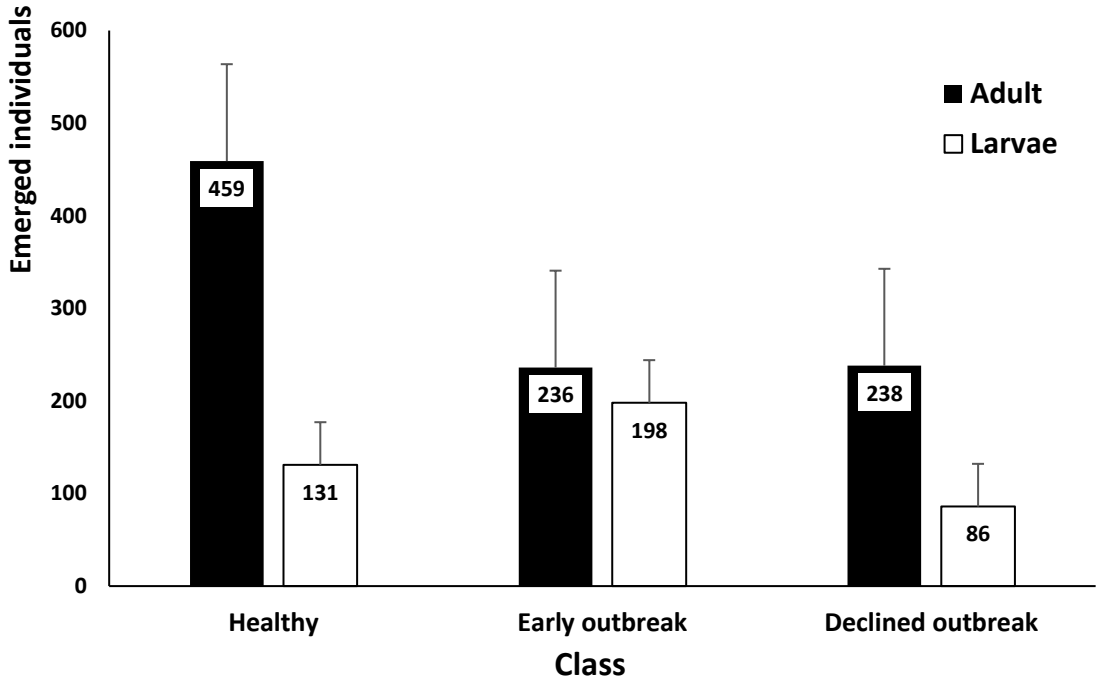

Fig. 13. Occurrence of family Staphylinidae (+s.d.). The early outbreak had more larvae compared to the declined outbreak, but no statistically significant results by Kruskal-Wallis test at 0.05-level were observed.

These emerged genera have interacted in earlier studies with bark beetles. Most adult staphylids emerged from the healthy class, the outbreak classes being close to equal to one-another (Fig. 13). As genus *Phloeonomus* comprises of 92% of all adult staphylids (n = 824), statistical analyses for whole family only represent the abundance of this genus. Larvae (n = 425) emerged most numerous in the early outbreak -class. Rove beetles emerging as larvae showed no statistical preference towards any class type (Chi square = 4.784, df = 2, p = 0.091) and only specific significant correlation was shown with adult rove beetles (r_s = 441, n = 27, p = 0.021) and *Epuraea* (r_s = 0.510, n = 27, p = 0.007).

Phoeonomus spp. were most abundant, and most likely majority of the larvae belong to this genus or Aleocharinae. Numbers of these species were significantly more numerous on the healthy class (Chi square = 6.362, df = 2, p = 0.042). Numbers were equal between the plots of both outbreak classes. Relative numbers (comparison to other beetles) on the contrary indicated that species actually was more numerous on the declined compared to the early outbreak class (66%/48% of all non-scolytinae beetles, Fig. 14). Genus was also the only antagonist group which itself had any statistically significant correlation with emerged spruce bark beetle (r_s = 0.424, n = 27, p = 0.028).

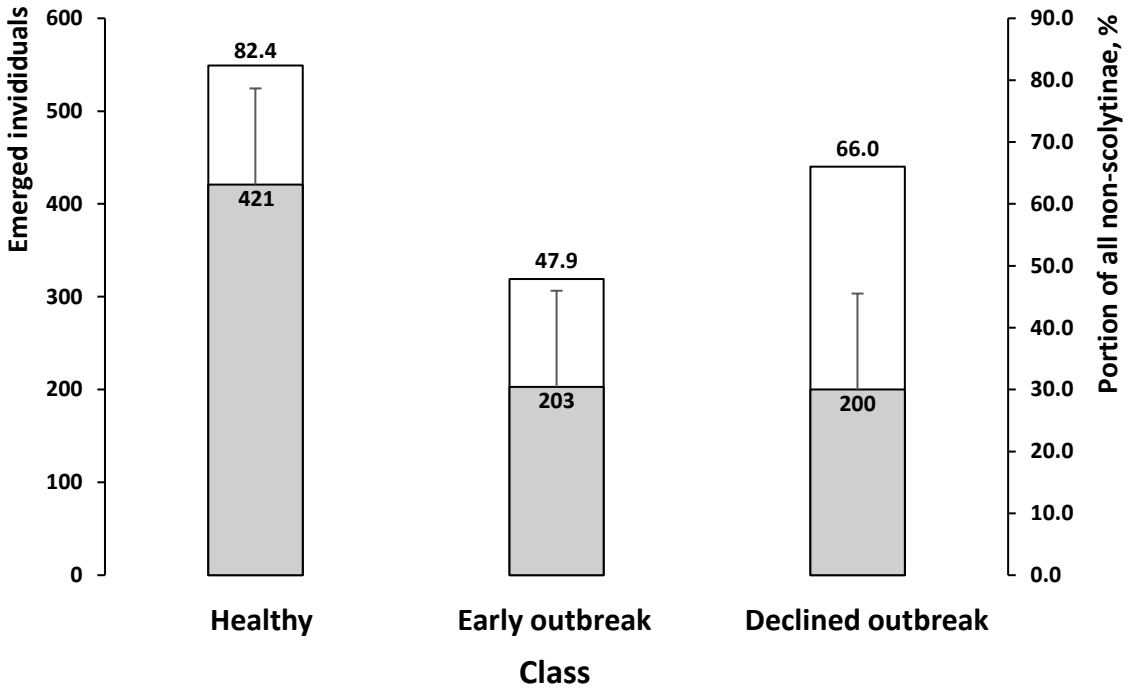

Fig. 14. Numbers of Phloeonomus spp. on different stand classes (grey, +s.d.) and their percentage of all emerged non-scolytinae beetles (white). While numbers between different stages of outbreak were equal, relative numbers in comparison to all other non-scolytid beetles were higher on the plots of declined outbreak.

Other rove beetles belonged mainly on the subfamily Aleocharinae, in the genera *Leptusa* and *Placusa*. *Placusa* was very limited in numbers compared to other small staphylids, although it was present in all stand classes. *Leptusa* preferred outbreak classes over the healthy stand, but failed to show any statistical difference. Aleocharinae was also analysed as a single taxonomic group. This combined taxonomic group showed significant correlation only to *Plegaderus vulneratus* ($r_s = 0.388$, $n = 27$, $p = 0.046$).

Larger species of Staphylinidae were less numerous. *N. lentus* did not emerge in quantities large enough to reach any significancy between any stand classes ($n = 10$). *Q. plagiatus* ($n = 28$) showed no significant relations towards any stand class. Differences were near significant, and numbers of *Q. plagiatus* larvae had statistically significant difference between the healthy and declined outbreak classes (Chi square = 8.500, df = 2, $p = 0.025$).

3.4.6. Elateridae – Click beetles

Due to a long lifespan of the group, only larvae emerged. Emerged larvae were mostly species *Athous subfuscus* and *Melanotus sp*., while single individuals of species *Paraphotiscus impressus* and *Denticollis linearis* where encountered. Due to small numbers, all click beetles were analysed as a single group. No significant differences between stand classes were detected in Kruskal-Wallis test (Chi square = 1.371, df = 2, p = 0.504), although the early outbreak had less individuals. This difference could have proven significant with larger sample.

4. DISCUSSION

4.1. Application of pheromone traps for monitoring *I. typographus*

Overall catch of the pheromone traps was very low compared to earlier observations. Weslien et al. (1989) observed that risk of damage is small unless group of three traps catch less than 15 000 individuals in one summer. Similarily, Niemeyer (1992) used amounts of 5000 *I. typographus* individuals annually and 300 individuals daily in a single trap as a risk limit. No single trap collected over 5000 individuals during summer (or 15 000 individuals for a trap group). That threshold most likely applies better in bivoltine areas of Central Europe. These risk limits have been developed in the Central Europe and Sweden, and studies for this threshold have not been conducted in Finnish conditions. Endemic population in the area was low after the year 2017, which is probably the main reason why population did not exceed this limit. While the conditions were very favourable for *I. typographus* in 2018, low reproductive population in the summer did not reach harmful levels. The second generation of beetles occurred in many area in southeastern Finland during 2018, but risk of damage remained low on the study area during that period. As weekly catches suggest that over 300 daily individuals per trap were temporarely reached in all stand classes, potential risk for a singletree-scale damage was still present.

While there was no statistically significant difference between trap catch of the stand classes, average pheromone trap on the healthy class gathered 25/19% less *I. typographus* than the early/declined outbreak class. Catch of individual traps varied greatly, and this explains why differences in analyses of variance were not significant. This supports earlier methodology that trap catch should always be inspected in groups of three traps.

4.2. Bark beetle success and competition in the logs

Bark beetles in the pheromone traps imply that the population of *I. typographus* was higher at the outbreak classes, which is contradictionary to the fauna in the trapping logs. The highest number of beetle individuals was found to emerge from the logs on the healthy stand class. There may be numerous reasons for this, but the amount of easily obtainable nutrition on the plots is probably the most important factor. The amount of weakened trees in the healthy class were non-existent, and the logs were the most easily habitable resource nearby. Both bark beetles and enemies concentrated on the few resources. On the outbreak classes, *I. typographus* was expected to attack weakened and recently dead trees. This was reflected in reduced overall numbers of all beetles attracted to the trapping logs. Numbers of adult bark beetles emerging from the logs were highest at the plots of the early outbreak class, but collapsed in the declined outbreak. In comparison to amount of bark beetles that were obtained in pheromone trapping, logs should have had more beetles at the declined outbreak class. This difference is most likely result of higher enemy impact.

Summer 2018 was exceptionally warm. Prolonged warmth induced second generation of bark beetles even as north as in Fennosscandia. It may be reasonable to expect this to have affected the logs. As ectothermic organisms, insects usually prefer warm open space over closed, shadowy canopy. This warmth benefited insects, shortening their lifecycle. In this aspect, it would have been expected to have increased numbers of beetles emerging from the logs in the declined outbreak class, where windthrown trees had left more open space in the canopy. Therefore results indicating that beetles emerged at higher numbers from the healthy class were surprising. Most likely this was due to the lack of obtainable phloem on the healthy site as mentioned earlier, forcing all insects on the same space. It was also possible that the healthy class received increased heat compared to average summer, creating optimal circumstances in normally too shaded environment. This is in

line with earlier observations, that *I. typographus* may prefer closed shadowy canopy in especially hot summers (Niemeyer 1997). Opposing effect is also possible. Lesser canopy coverage and increased exposure to sunlight may have dessiccated phloem in the declined outbreak class. I.e. emergence in the healthy class was not exceptional, but instead the declined outbreak class had suboptimal conditions. While drought makes trees more susceptiple to attacks, it has also been pointed out that may reject too dessicated trees (Netherer et al. 2015). The healthy and early outbreak classes were more similar, having no windthrown trees and earlier disturbance. That would explain quite an equal total amount of enemies in these classes.

Most of the emerged insects were bark beetles. Competition between bark beetle species was not detected in this study. In general, correlation analyses gave positive outcomes, i.e. success of one species benefits others. While logs in the healthy stand had the most emerged individuals althogether, this was not evident for *I. typographus*. Great part of the phloem was inhabited by *D. autographus* at the healthy class. Considered the ecology of the species, *D. autographus* most likely occupied space left by *I. typographus* population. Since *I. typographus* was not numerous enough to use all of the phloem at the healthy class, *D. autographus* was attracted to the remaining part. This is supported by the result, that the correlation between two species was non-significant.

It was logical that *I. typographus* was less numerous at the trapping logs of healthy class and most numerous at the early outbreak class. It was assumed that population was at highest at the early outbreak class, but regulators and lack of resources had lowered the population at the declined outbreak class. Increased amounts of weakened trees with fresh phloem had increased the population of the bark beetles on the outbreak classes, which was demonstrated by the pheromone trap catch. This case was also seen in natural enemy populations, since predators had not yet reproduced in sufficient numbers to regulate suddenly increased bark beetle population in the early outbreak class. On the contrary, regulators had reproduced in earlier years, and population of enemies regulated bark beetles more effectively at the declined outbreak class. This caused trapping logs of the declined outbreak class to have lower number of emerged *I. typographus* individuals in comparison to the early outbreak.

Since colonization was forced by settling, *I. typographus* was able to get a good start before any other insect could find the logs. This and bark thickness may explain why usually more common *Pityogenes chalcographus* (n = 13) was low compared to earlier studies and summaries (e.g. Niemeyer 1997, Hedgren and Schroeder 2004). *D. autographus* had occupied space in the trapping logs of healthy stand, were *I. typographus* did not emerge in numbers sufficient to utilize whole phloem. *Crypturgus* spp. were encountered in greater numbers in the declined outbreak. The result was expected, since genus is found in older wooden material and branches years after initial disturbance (Nitterus et al 2004). This kind of material was most abundant at the declined outbreak. *Crypturgus spp.* also showed significant correlation with *I. typographus*, which strongly proves that this scolytid beetle is not a competitor. On the contrary, this genus benefits from its associate. No correlation or significant differences between stand classes were found in statistical tests, leaving stand preference to speculation in this setup.

These results support the idea, that these common bark beetle associates did not have effect on the success of *I. typographus* during the first year of outbreak, and these species are not competitors. Potential competitors were almost absent in this study, indicating that potential competitors cannot compete for space in logs already inhabited by early *I. typographus*. Furthermore when the settling of the logs was complete, flight of these potential antagonists was possibly over. Other potential competitors were not identified among the emerged insects due to small numbers. Beetles of Cerambycidae remained in the logs until the experiment was over. As a slowly developing species, it had no effect on fresh deadwood. This makes intraguild omnivory unlikely for this species, at least in effect large enough to affect *I. typographus* success. As other beetles were not effective competitors, intraspecific competition was the only potential form of competition.

4.3. Emerged species

4.3.1. Thanasimus spp. - Ant beetles

Ant beetles are classified as obligate predators in literature. Species being most common in the healthy, managed stands is mostly in line with earlier studies (Schlyter and Lungren 1993, Hilszczański et al. 2007). Even if numbers of individuals were low, *Thanasimus formicarius* have high potential impact due to the high consumption rate of bark beetle

larvae. There are many explanations why the number of the individuals was so low. Adults are active early during spring, and primary mating of ant beetles may have already passed when the logs were exposed to local fauna. On the other hand, Gauss (1954) noted that ant beetles oviposit during extended period. While most of the oviposition had happened during spring, some ant beetles were active later. As this reproduction happens most likely in fewer numbers compared to early summer, this would explain why we observed such a low number of ant beetles in this study. In addition, other studies have used pheromone baits that have been attached into logs instead or in addition to inhabiting *I. typographus* (e.g. Weslien 1992a). This means that the numbers of *Thanasimus* may also be lower due to the weaker kairomone-effect. This is very likely to be evident for other antagonists as well. Finally, numbers of all emerged insects were generally higher in the healthy stand, which may be one reason why the species was also more numerous in the healthy class. There were more prey at logs in the healthy stand, implying that difference between the healthy- and declined outbreak classes is a cause of an overall amount of insects.

While this study does not explain exactly why the ant beetle was completely absent in the early outbreak class, there are reasonable explanations supported by earlier studies. It is probable, that as *I. typographus* breeds faster than this semivoltine predator, population of the ant beetles had no time to react into increased population of the bark beetle. Since *I. typographus* is capable of escaping in space (Schroeder 2007) and reproducing rapidly, semivoltine populations of ant beetles have been too inflexible to react increased population density at the early outbreak. Endemic population of ant beetles was too small to inhabit all infested trees and logs at the early outbreak. On the contrary, the declined outbreak class have had increased *I. typographus* populations for several years, allowing ant beetles to reproduce and shift between infested trees. The declined outbreak had other infested trees besides the logs, and therefore not as great portion of ant beetles colonized the trapping logs in comparison to the healthy class.The healthy stand was example of an opposite phenomenon. While populations of both *I. typographus* and *Thanasimus* were low, so were the number of infested trees. Since the healthy class had no other easily obtainable phloem, logs attracted effectively all bark beetles and associates on the class. As the numbers of trapped *Thanasimus* individuals in the pheromone traps have been greater in the disturbed forest sites (Weslien 1994), this would explain why it was not evident for the trapping logs. This theory should be tested with larger sample.

Claims that *Thanasimus* larvae are incapable of pupating under spruce bark (Warzée et al. 2006, Thomaes et al. 2017) are supported by this study. Larvae abandoning logs before winter indicate that species seeks better pupating and overwintering location than these *I. typogaphus* galleries it inhabited during summer.

Thanasimus formicarius with semivoltine lifecycle was expected to be more common at the declined outbreak. This was due to assumption that secondary bark beetles in the declined outbreak would sustain higher population of ant beetles in comparison to the healthy and the early outbreak –classes. Instead it was more apparent, that *D. autographus* in the healthy class could be alternative food source. There was a positive correlation between *Thanasimus* beetles and *D. autographus* to support this. As a long living and slowly growing predators, ant beetles require constant source of prey. *D. autographus* is relatively late colonizing the space, and may therefore serve as a food source for ant beetles in late summer.

4.3.2. Histeridae – histerid/clown beetles

Distribution of *Plegaderus vulneratus* at the stand classes followed well the numbers of *I. typographus*. Exceptional compared to other predators, *P. vulneratus* was also significantly more common at the early outbreak class. According to this data, it is likely that *P. vulneratus* can quickly adapt to increased number of prey. The classes of healthy and the declined outbreak had statistically similar occurrences of the species. The species have been on the flight relatively late in earlier studies (Weslien 1992). In comparison, many obligate predators were already met in pheromone traps before settling of *I. typographus* had even started. This means that impact of the *P. vulneratus* on the first generation of *I. typographus* may not be notable.

Plegaderus vulneratus consumes eggs and larvae. *P. vulneratus* adult and larvae were encountered in logs relatively late summer, similarly as in Schroeder and Weslien (1994). Late finding of the *P. vulneratus* larvae indicates that species still feed on either eggs and larvae of the second generation of the bark beetles or larvae of other insect orders. Numbers of emerged larvae other than bark beetles were still numerous when logs were sealed. While there was no correlation between emerged dipteran larvae and *P. vulneratus,* soft larvae might be an additional source of food. That would also explain

why so many histerids were still present at autumn. Earlier studies in Central Europe indicated that Histerids commonly overwinter in the bark beetle galleries and emerge in spring (Wermelinger et al. 2012). In this experimental setup, almost all individuals left the logs in late summer. This difference may be a cause of the different winter conditions, adult beetles leaving logs to overwinter under snow cover similarily to *I. typographus* in the northern conditions. On the other hand, this might also be a difference between the two species. According to Wermelinger et al. (2012), most of the histerid beetles were species *Paromalus pallelopipedus*, while in the current experiment only *Plegaderus vulneratus* was encountered. *P. vulneratus* was very common compared to earlier studies. Weslien (1992) observed that there were hardly any individuals in the logs after eight weeks of exposure in the early summer. Time of exposure was a lot longer in this study. These differences indicated that the species colonizes galleries of *I. typographus* relatively late. This raises a suspicion whether the species has any significant influence on reproductive success in Northern Europe. As second generation of *I. typographus* is still relatively rare in Fennoscandia, late occurring predator of eggs and larvae have only small effect on the population dynamics during the first year after disturbance. Should the second generation of bark beetles become more common in Fennoscandia, histerids become very important regulators of *I. typographus*.

Interestingly, genus *Plegaderus* showed correlation with beetles of Nitidulidae, which emerged mostly as a larva. As correlation was strong, this might imply of relatively similar feeding strategy or habitat requirements. The small numbers of histerid genus *Platysoma* are most likely due to the lack of pheromone bait on the logs. This phenomenon has been encountered in previous studies comparing baited and un-baited logs (Schroeder and Weslien 1994).

4.3.3. Nitidulidae – Sap beetles

Different species of sap beetles were on the flight relatively early, being encountered on the pheromone traps in May. On the contrary, sap beetles have been encountered relatively late on the bolts (Wermelinger 2012), from where these left in late summer. There is no clear explanation why nitidulid beetles abandoned logs as a larva in this study. Most likely these larvae encountered in the logs were species that leave trees to overwinter and pupate on the ground level in Finnish conditions. Adults were most likely

overwintered individuals, breeding and feeding in galleries. It can also be speculated that forest management has affected nitidulid population by removing trees in which the genera overwinters, causing adaption to exit logs early. That would explain why a few adults emerged still relatively late, only from the logs of the declined outbreak class. This is not easily proven, and it is more likely that adults were simply breeding individuals during summer that remained in the logs afterwards. Earlier studies implied that adults could remain in logs feeding on *I. typographus* eggs (Nuorteva 1956), although the current study does not support this. Small number of adults is in line with earlier observations, as numbers of adults have been insignificant compared to larvae (Weslien 1992a).

Epuraea was slightly oriented towards the declined outbreak class. It was also the only genus that had such preference. This difference is even clearer, when comparing to relative numbers of all beetles and *Epuraea*/*Ips*-ratio. This implies that genus could benefit from excess deadwood on the stand or at least delay from collecting windfelled trees. Similarity of the healthy and the early outbreak indicated that genus is slowly increasing as health status shifts towards more severe infestation. Nitidulid beetles are therefore not efficient population regulators, as the highest occurrence in the declined outbreak class implied that potential regulation happens with too long delay. This genus of sap beetles does not adapt on increased numbers of bark beetles until later years. On the contrary, Nitidulidae would clearly benefit from constant deadwood and secondary bark beetles, making it ideal target for management practises. As family did not breed fast enough to show increase in population density during early outbreak, it would be beneficial to keep endemic population induced by constant prey and deadwood continuum. As these beetles are not usually considered highly voracious, the biggest question is their true impact on their occasional prey. Simultaneously, *Epuraea* larvae themselves were preyed upon in Weslien's experimental setup (1992). If other predators limit potential of the genus, then its impact is hardly worth inspecting.

4.3.4. Rhizophagus spp. – Root-eating beetles

Monotomid beetles from genus *Rhizophagus* are most likely omnivores. The current study showed no proof that genus preys actively seeks the bark beetles, and results support the idea that genus might only be opportunistic predator in addition to its fungal diet. In

this study, only *R. dispar* matured before emerging. This makes assessing predatory impact and stand preference difficult, as this specific species is one of the least certain predators. Larvae were left unidentified, but most of these are also likely to be *R. dispar*. While the number of emerged beetles on the plots of the early outbreak were double compared to the other stand classes, this should not be taken as an indication of difference. As individuals were concentrated only on a few logs, it is likely that conditions in those specific logs were ideal, instead of the stand class. While logs were identical, differences in microclimate may have affected humidity and heat exposure in phloem. Combined to earlier speculation whether species is voracious or not (e.g. Merlin et al. 1986, Hedgren and Schroeder 2004), this study does not support idea of this species being an efficient regulator. While species was most frequent at the early outbreak, it did not show any correlation with *I. typographus* or other bark beetles. More interestingly, it had remarkably many negative correlations. It was more frequent in the logs where less other predators emerged. These correlations did not flag any single species, but suggest that other predators could have cumulative reducing effect on this genus.

4.3.5. Staphylinidae – Rove beetles

High abundance implies that rove beetles are either strongly associated to Scolytinae, as a predator or scavenger, or utilize the habitat created by bark beetles. Most likely both, as diverse family has well known predators, but also numerous omnivores.

Phloeonomus spp. were more numerous at the healthy stand. As *Phloeonomus/Ips*-ratio was higher in plots of the declined outbreak, there could still be some notable increase in numbers of this genus in these disturbed sites. This is still a speculation, since it does not explain why numbers have decreased already in transition from the healthy stand to the early outbreak. This difference may be a cause of limited resources, which led to these staphylids to concentrate on the trapping logs in the healthy stand. The impact of the genus on the *I. typographus* must be relatively opportunistic, as species emerging in such a high numbers should have otherwise had strong reducing effect on the bark beetle population. Genus correlated with *I. typographus*, but this is most likely due to fact that bark beetles create suitable conditions for it. Species even had stronger correlation to the second most abundant bark beetle *D. autographus* (Appendix 2).

Quedius plagiatus and *Nudobius lentus* are relatively well-known examples of predatory species inside the bark beetle galleries. *Q. plagiatus* larvae being more common at logs in the healthy class, results signal that it prefers shadowy environment to open disturbed sites like the declined outbreak class. This is in line with observations by Johansson et al. (2007). If sample size were larger, all lifestages would have most likely proven statistically significant preference. For *N. lentus* it was not possible to test if opposite preference of openings was true in the current study. Similar to *Q. plagiatus*, *N. lentus* was more common at the healthy stand, but that difference cannot be verified due to low frequence. *N. lentus* is known to be very common and important predator, and these numbers imply that trapping method or timing fit poorly its occurrence. It is also possible, that larvae of the species were not identified from other staphylids. These two predatory species clearly occurred in the healthy stand, which also applies to predator/prey-ratio. In this aspect, *Q. plagiatus* showed similar performance to *Thanasimus* ant beetles. It is also possible for these genera to have reduced numbers, as kairomone effect was not strong without attached pheromones.

Staphylinidae larvae did not show statistical significance, even as numbers were greater at the early outbreak. Their numbers can be still used to indicate, whether differences of adult beetle occurrence were true, or differences were results of rove beetles being in a different development stages in a different stand classes. There might be some truth in that: In comparison, the healthy stand and early outbreak were similar in structure as attack on the trees was just about to begin. When both larvae and adults were inspected, differences were no longer statistically significant. This implies that common staphylids, mainly *Phloeonomus spp.*, were perhaps not more common at the healthy stand, only further in development. While numbers of staphylids decreased when health status proceeded to infestation, so did numbers of all insects. This did not imply the significant difference of staphylids, but instead correlated with success of habit-creating scolytids.

4.3.6. Elateridae – Click beetles

Analysing click beetles as a single group is very questionable. Most common emerged species *A. subfuscus* is not known as a predator, but mentioned as omnivorous (Strey 1972, Schauermann 1977). It is also a very common species in a soil (Schauermann 1977),

which means that scolytids are most certainly not a frequent prey for it. Genus *Melanotus* is more probable to encounter and feed on the larvae.

Click beetles emerging in the healthy and declined outbreak classes were over three times more numerous than in the early outbreak. This generally leaves expression that slow growing insects did not react fast to the increased bark beetle population, but instead used generalist prey in both the healthy and declined outbreak classes. Relative numbers also showed similar results with even greater weight on the declined outbreak. Click beetles represented 1.3 percent of all non-scolytinae beetles emerging from the healthy class, 2.3 percent of the declined outbreak class, but only 0.5 percent of those in the early outbreak class. Actual frequencies on the other hand showed no statistical significance, which is most likely due to low number of individuals. On the contrary, pheromone traps seem to bait higher amount of click beetles. This issue should be assessed in the later studies, as it is uncertain whether these are baited by the pheromones (kairomone effect) or rotting carcasses. Low numbers in this study indicate that click beetle larvae have no significant effect on the *I. typographus.*

Of all predators in this study, only elaterid and ant beetles are semivoltine. While Elateridae had correlation with ant beetles, semivoltinism seems to be the only common factor between these two families. In a case of the elaterid beetles, lifecycle from egg to adult may even take three or more years. While ant beetles are usually mentioned as the most important predatory beetle genus, click beetles have generally not been noted as a predator, as many species are herbivores and some species are agricultural pests. However, if click beetles are opportunistic, generalist predators, their long life cycle means that these require several prey before maturing. For *I. typographus,* this family has no significant effect. Usually phloem resources are depleted within a year or two, and *I. typographus* occupies the same space for only a short period.

4.4. Natural enemies - synopsis

Compared to many other studies, the catch of natural enemies seems to be very modest. It is very likely that pheromones attached to the logs in the earlier studies had significant effect, implying that kairomone effect is significant for the predators. Settled initial *I. typographus* population was perhaps not optimal for attracting and sampling enemies.

Many beetle families seemed to prefer the healthy class. This may be a fact in some cases, as in earlier studies e.g. *Thanasimus* ant beetles have had greater impact in managed stands (Schlyter and Lungren 1993, Hilszczański et al. 2007, Schroeder 2007), of which the healthy class represents in the current study. This assumption should not be made collectively for all enemies. Some of these families cover remarkable portions of data, e.g. genus *Phloeonomus* consist of 82% of all adult enemies in the healthy class. Combined numbers of all coleopteran predators mistakenly show slight trend where numbers of predators are high in the healthy class, decreasing as forest health shifts to more severe infestation. As both obligate predators (ant beetles) and omnivores (staphylids) were most numerous in the healthy class, even healthy stands seems to have variety of different antagonists. Due to the great numbers of both natural enemies and secondary bark beetle species *D. autographus* at the healthy class, possibility of it being alternative prey species cannot be ignored. The current study suggests but leaves open the question if measured stand preference is only a cause of limited space, directing all phytophagous insects and predators to limited resources.

Results in general did not support the idea that natural enemies are homogenous group whose numbers would follow numbers of *I. typographus*. As total numbers of enemies were very similar between the healthy and early outbreak classes, differences between these classes were partly cause of the different life stages of the enemies. This study supports earlier assumptions concerning many feeding habits of natural enemies. Many facultative predators feeding on the larvae, mainly *Plegaderus vulneratus* in the current study were not as common at the healthy class as the antagonists on average. This may be a cause of that stand class having no significant amount of earlier prey present. Many facultative species were more common at the outbreak classes. This applies to families like *Rhizophagus spp*., but results are harder to justify. As all adults were *R. dispar* and results were not statistically significant, impact of this species is unknown. The same was also evident for the genus *Epuraea*. These species were expected to correlate with other suitable prey, but no correlation to other larvae (mainly Diptera) was detected. This may indicate that a diet was so balanced generalist predation, that no single source of prey was highlighted in the correlation analysis.

4.5. Significance of the results and potential for forestry

Applications of these results to forestry are questionable due to being only a single study, although some conclusions can be made. It was assumed that enemies would increase as health status shifts into more severe outbreak. It did not seem to be the case, but instead the numbers of natural enemies and predatory pressure seemed to be highest at the healthy class. This means forest management and sanitation forces the bark beetles and enemies into same space, potentially increasing mortality caused by predators. This supports the use of sanitation loggings, as it seems to regulate bark beetles effectively by reducing suitable space and potentially exposing these to predators. Even as the healthy class had more enemies and lower prey-predator ratio, this may not be that simple. In the declined outbreak, numbers of emerged *I. typographus* were very low compared to numbers in the pheromone traps. This means that mortality caused by enemies has most likely been higher than enemy occurrences indicate.

Of the genera inspected, histerid beetles seem to have the most potential as a control agent. Great numbers imply that *P. vulneratus* could reproduce fast enough to affect reproduction of *I. typographus*. This may not save the infected trees, but overall health of the stand may increase as numbers of regulators are temporarily enhanced. If these beetles have significant effect on the bark beetles, i.e. can be shown to consume significant amounts of bark beetle larvae, these should be taken into consideration in management practices. *P. vulneratus* seemed to prefer outbreak classes, which means it could benefit from a few infested trees left standing. Species also left trapping logs relatively late, which means that this enemy species would have been removed from the stand if windthrown trees that these logs represent had been collected in sanitation loggings. As *I. typographus* individuals are already mature in the late summer when histerids were most numerous, enhanced regulator population seems to have an effect during next year at earliest. This time lag is significant, but it does not mean that the pest can rise into harmful levels before regulators have an effect.

Bark beetles utilize the windthrown trees after the disturbance before moving into standing trees (Gall and Heimgartner 2003, Komonen et al. 2011). Natural enemies are likely to begin reproducing in the same weakened or wind-felled trees in which the bark beetles feed on and reproduce in. This means that enemies, which reproduce in significant

numbers during the first year after the disturbance, are likely to have effect on the *I. typographus* population that starts attacking the standing trees. According to results, at least *P. vulneratus* seem to have already reacted in numbers before overwintering. Using histerids is not a new idea, since earlier studies have inspected North American species as a biocontrol agent (Shepherd and Goyer 2005). Releasing adult beetles into pest outbreaks could reduce offspring of bark beetles, but the method is not often used in the context of forest management. Breeding predators in the captivity and allocating them is costly, and forest stand is open ecosystem in comparison to greenhouses. This treatment should also be repeated in multiple times before harvesting timber. Using bio-control agents in the same way they are applied in the greenhouses would prove inefficient at the current state of management practices and timber value.

In the current study, numbers of *P. vulneratus* showed rapid reaction to increased bark beetle population, probably affecting the population notably already in the second summer. Manipulating stand attributes by leaving a few infested trees until autumn could increase the pressure from this species. Overall, sanitation loggings may still seem to be efficient way of preventing damages. Timing is very important. If loggings are late, i.e. generation of *I. typographus* has already left the logs, it could be beneficial to leave those trees standing or remove them later during winter. This way e.g. *P. vulneratus* leaves trees before being removed. As most of the enemies in this study left logs and overwinter elsewhere, removing trees in winter would not affect notably the population of the enemies.. Sanitation loggings are still often required. It is possible that the pest population density increases too rapidly for the natural enemies to regulate early. During such wide-scale disturbances, limiting the potential breeding material also forces pest and the predators into same space. For this reason, decision to start loggings depends on the estimation whether the damage caused by the pest during next year is greater than damage caused by the machinery in sanitation logging.

4.6. Possible sources of error

4.6.1. Neglected biotic regulators and other factors

Along the beetles, over three thousand other larvae emerged from the logs. Most of these belonged to the orders Diptera and Hymenoptera, although specific identification of these

larvae was not possible. Some of these would even require DNA-sequencing. A proportion of these represent predators or ectoparasites, while others are feeding on phloem or hyphae. Usually dipteran genera *Medetera* and *Lonchaea* are mentioned as important predators of the spruce bark beetle larvae, while hymenopteran genera *Rhopalicus, Roptrocerus* and *Dinotiscus* are important parasitoids. On the other hand, their significance as a controlling agent is debatable. While *Medetera* is mentioned to be important enemy, in Mills (1985) experimental setup the predation portion of the genus was less than 5%. As *Medetera* larvae feed on the scolytid larvae that may already be infested by parasites, their impact is lower than numbers would perhaps imply. These phloem feeding and scavenging larvae on the other hand, are one possible prey for generalist predators. Numbers of scolytid beetles may therefore not be the only factor explaining the abundance of the predators. Instead of the scolytids, dipteran larvae could serve as late prey for the predatory beetles. The importance of coleopteran predatory species is hard to measure, since their feeding habits are usually facultative (Johansson et al. 2007). While laboratory tests have proven the mentioned predators to feed on *Ips* larvae, these might also be feeding on e.g. dipteran or hymenopteran larvae. It is impossible to distinguish which prey the predators are using in field experiments. Settling was made to counter this issue, in order to ensure numbers of spruce bark beetle were higher than other prey, although this was no longer certain in late summer. In addition to other insect larvae, mites were left unidentified. Often mites disperse by being attached to bark beetles, being phoretic ectoparasites (Hodgkin et al. 2010). While these use beetles to find new habitats, they also parasitize eggs (Lindquist 1969). Both insect larvae and mites had the same issue in this study. As detri- and fungivores were not identified from antagonists, potentially important relations were disregarded.

One factor that may affect the results of this study are the scattered forests of Finland. United, vast areas of homogenous forests are quite uncommon, especially in the southern parts of the country. All of the plots were close to one another to reduce climatic variation. At the landscape level, plots are still on the similar geographical area. While conditions clearly altered between plots and classes, one may argue that the Finnish forests are so fragmented, that on a larger scale study areas did not differ from one another. Most importantly, this means that there might have been exchange of insects between areas with different forest health statuses. While this was countered by keeping stand classes separate, plots had to be close one another in order to eliminate the geographical variation.

This could lead into conclusion, that observed differences are the cause of a different microclimatic or temperature based -conditions, not management or disturbance related issues.

In management aspect, buffer zones of 500 metres from infested site is considered sufficient (Angst et al. 2012). Earlier studies indicate that *I. typographus* prefers to attack nearby trees, but can fly over a kilometre in search for new brooding sites (Botterweg 1982, Zumr 1992). This most likely means several kilometres with favourable wind conditions. Austaråa and Midtgaard (1986) speculated that migration would be considerably large from three to four kilometres. Migration of tens of kilometres has been recorded (Nilssen 1984), although numbers of individuals travelling this far are probably insignificant compared to local populations. The dispersal abilities of most natural enemies are not studied (Kenis et al. 2004), and therefore it can only be speculated whether they can fly as long as their prey. In Finland, similarly structured forests with diameter of at least one kilometre are rare outside of conservation sites in Lapland. For this reason, there is always a possibility that on the landscape level there are no differences between occurrences of natural enemies. In order to test this hypothesis, study should be replicated in more homogenous landscape. This information could be used to avoid bark beetle outbreaks by planning forest management on the landscape level. On this scale, the results of pheromone trapping are more plausible (Niemeyer 1992).

4.6.2. Evaluating trapping logs as a monitoring method for natural enemies

Settling was originally chosen for several reasons. Year 2017 was exceptionally humid. After a cold and humid year, and without a recent stock of wind-felled trees, population of *I. typographus* was expected to be in decline on the landscape level in the whole area of Eastern Finland. This phenomenon could lead to few different scenarios. Some logs might get scores of beetles, while others be colonized later or remain untouched. Results would only depict population of *I. typographus,* but interactions and natural enemy complex would also alter according to success of colonization by endemic *Ips*-population. In order to inspect differences between stand classes and forest health influences, all logs needed successful colonization. Settling also gave flexibility in choosing plots. It proved relatively difficult to find newly infested areas after a humid year, when all known outbreaks had either declined or had sanitation loggings. Signs of colonization in trees

were not visible from early to mid May, when beetles began swarming. It was not possible to take logs into forest until late May, since the lack of indicators would have increased the possibility of falsely identified stand classes. Suboptimal conditions in the previous year also may have had negative effect on the populations of natural enemies, especially for those which are dependent on flying (parasitoids).

The trapping method itself has issues, which affects the fauna encountered in emergence traps. As numbers of emerged *I. typographus* were lower at the declined outbreak (most likely regulated by enemies), pheromone traps were required to gain evidence of the overall population level of the bark beetle. Traps proved that population of *I. typographus* was higher than individuals emerging from the logs would indicate. Unfortunately, it cannot be tested if some natural enemies were affected in a similar manner, being more common than emergence traps indicates. The method also assumed that predators and other natural enemies are active by their habits, emerging from the logs as adults or accidentally during earlier life stages. In this aspect, the method measures insect groups that are active, and leave logs when either maturing or leaving for overwintering. Numbers of emerged enemies are most likely not an adequate way to measure enemy impact (Schroeder 2007), unless all beetles are caged for the whole study. Insects emerging during spring were also collected for this study, but only fauna emerging before November 2018 were inspected statistically. Of most of the less known genera, it is unknown whether species overwinter inside logs in Finland. This can be later assessed according to emergence data from the spring. This may also vary annually depending on conditions, and could be an issue in future studies.

This method captured only natural enemies preying on the later generations of bark beetles. While it is suggested that timing was correct, as both bark beetles and natural enemies emerged from the logs, there is always possibility for some rapidly developing genera to have escaped the logs before caging. This is possible for genera with rapid life cycle, which have been met early in the pheromone traps like *Epuraea* (Weslien 1992a). The problem is, that method captured only one temporal moment, and is incapable of estimating whether or not different natural enemies already left the logs. This could affect the numbers of several predators with univoltine or faster development cycle. This would explain small numbers or absence of some species in the data (e.g. Tenebrionidae: *Corticeus linearis*). Sealing was aimed for the moment that maximized the time for

predators to colonize the logs. Since emergence and temporal patterns of different enemies vary (as stated by Wermelinger et al. 2012), it is impossible to determine the differences in fauna without having logs caged during different periods of summer. Since there were differences between individual logs, these twenty-seven logs would have been insufficient to be divided temporally across the summer. Therefore increasing the amount of logs would have been the only option for adding temporal aspect. This was not possible in the current study areas, but could be added in the future studies.

Timing of the caging in the late summer was an important factor, but so was the timing of settling in early summer. The mass flight began in mid-May. Logs were exposed to natural enemies at the end of May. This means that some of the earliest natural enemies, mainly overwintered generalist predators, had already swarmed during the settling. For some species, this is not exactly a problem. For example, ant beetles emerge early, but oviposit their eggs through the summer (Gauss 1954). This means that while logs missed the first individual breeding females, there were still equal possibility for each log to be inhabited later. Other not so well known species on the other hand may not be as fertile, meaning that logs missed the first and only swarming of possible natural enemies. Most of the known enemies from the literature were captured, implying that the species that would have been affected by the timing are not well known. Species that have flight later on summer may also have had better chance of finding prey, affecting results.

4.7. Outcome of the hypotheses

In the current study, the following underlined hypotheses are accepted:

1) **H_0= Numbers of natural enemies are not greater in the outbreak classes compared to the healthy reference.**

   H_1= Numbers of natural enemies increase as forest health shifts from healthy to more severe infestations.

No significant difference between numbers of enemy species were detected between stand classes. While there were more enemy species on the declined outbreak in comparison to the early outbreak, the healthy class had most species. Same trend was detected in the total numbers of beetle individuals. As there were no difference between

stand classes according to Kruskal-Wallis test, total number of the enemies is considered equal between all stand classes. Even opposite phenomenon is possible, as the healthy class had slightly more enemy individuals. **H_1** should therefore be rejected.

2) **H_0**= Enemy species are not affected by the health status of the stand. Conditions in the inhabited tree are more important.
   H_1 = There are enemy species which are affected by health status of the stand.

If **H_0** were to be retained, differences between occurrences of enemies should be random between individual logs. As logs were similar in quality, all differences between results are cause of stand properties and local populations. In this study, three genera had significant preference to logs of certain stand class. Even if *Thanasimus* -beetles are rejected due to the small sample size, genera *Phloeonomus* and *Plegaderus* clearly proved **H_1** hypothesis correct.

3) **H_0 = Natural enemy populations can adapt to the increased *I. typographus* population already during the first year of *I. typographus* outbreak.**
   H_1= *I. typographus* reproduces faster and outbreed its enemies. Natural enemy populations respond with delay to increased bark beetle numbers.

H_1 hypothesis assumes that enemy escape hypothesis always applies to *I. typographus* and natural enemy complex (Schroeder 2007). **H_0** assumes that natural enemies are capable of responding in early population growth of *I. typographus*. In order to **H_1** be accepted, several assumptions should be evident. The healthy and early outbreak classes should have had equal numbers of enemies. Enemies had no time to respond to increased bark beetle population at the early outbreak class, so enemy complex should resemble the healthy class. While this was correct when the total number of enemies were compared, many individual enemy species had different distribution. More importantly, **H_1** assumes that enemies at the declined outbreak class had time and resource to increase in numbers, as outbreak had started in previous years. No enemy species had significant preference to the declined outbreak class, while the total amount of enemies was also lower. **H_1** should therefore be rejected.

5. CONCLUSIONS

The current study provides insight for certain forest management aspects. Three species groups having significant preference for the stand class proves that health status affects the natural enemy complex. Most likely many other species have some sort of specific preference, which was not proven due to small sample size. Opposed to all assumptions, no species was statistically proven to prefer the declined outbreak class. This result is surprising when compared to paradigms. Natural enemies are assumed to have grown in numbers on the declined outbreak class representing disturbed forest stands. Even if enemies were more plenty in this storm disturbed stand class than these results imply, predators were unable to effectively colonize the newly *I. typographus* infested trapping logs. This means that in order to make correct conclusions, other methods of sampling must be compared to these results. This may mean other trap types or taking similar logs from the trees of the plot instead of bringing these from somewhere else. Influences of the kairomone-effect have been proven important, and relatively low catch of the enemies compared to earlier studies suggest that pheromone lures should be used.

Enemy species being more common at the healthy stand seems to support the sanitation and salvation loggings as a method of control. More important would be to resolve the cause behind this phenomenon. If this arisen postulate about limited resources directing bark beetles and predators effectively into same space could be proven, this could even further promote forest sanitation and active management. On the contrary, logs of the declined outbreak had less emerging bark beetles, despite the fact that pheromone trap catch indicated higher *I. typographus* population. This means that enemy induced mortality may still have been greater than the current study could measure. Issues with damage caused by the sanitation loggings and resulting losses due to pathogens would still require other solutions.

True management potential of the enemy complex remains unclear. While genera *Phloeonomus* and *Plegaderus* were able to rapidly reproduce in the early outbreak class, true impact of these species on the *I. typographus* is still relatively unknown. A few pieces of deadwood could sustain higher number of these enemies, but many forest owners are more likely to still utilize safer sanitation methods that are currently in practice. The lack

of correlation between *I. typographus* and most predators proves that bark beetles can outbreed predators in the first years after the initial disturbance. Strong endemic population of enemies would be required to keep up with the pest. As *Plegaderus vulneratus* was the only species that increased in numbers at the early outbreak class, it is probable that small scale damage is inevitable before these regulators affect the success of *I. typographus*. Excluding the ant beetles, predators seem to be very generalistic in their diet. Even if some the generalistic predators were more abundant in the declined outbreak than these results indicate, these seem to colonize newly infested trees too inefficiently to fill needs of the forest management.

Annual variation in accumulated temperature within and between summers may influence the natural enemy complex. This makes generalizing these results difficult, as long-term data is difficult to obtain. Eruptive nature of the bark beetle outbreaks means that plots classified as an early outbreak may resemble next year more of a declined outbreak class. As such, there are still many uncertainties conserning the results.

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Includes material from Finnish national land survey (08/2019)

Appendices

Appendix 1: Coleopteran species and genera encountered in trapping logs.

Species (auk, year) number of emerged individuals

Scolytinae

Hylurgops palliatus (Gyllenhal, 1813) 7

Hylastes cunicularius (Erichson, 1836) 14

Pityogenes chalcographus (Linnaeus, 1761) 13

Ips acuminatus (Gyllenhal, 1827) 1

Ips duplicatus (Sahlberg, 1836) 6

Ips typographus (Linnaeus, 1758) 4875

Dryocoetes autographus (Ratzeburg, 1837) 1223

Dryocoetes hectographus (Reitter, 1913) 2

Crypturgus spp. (Erichson, 1836) 509

Orthotomicus laricis (Fabricius, 1792) 1

Orthotomicus suturalis (Gyllenhal, 1827) 29

Trypodendron lineatum (Olivier, 1795) 1

Predators and potential antagonists

Thanasimus formicarius (Linnaeus, 1758) 17

Plegaderus Vulneratus (Panzer, 1797) 271

Platysoma angustatum (Hoffmann, 1803) 2

Epuraea (Erichson, 1843) 53

Epuraea cf unicolor (Olivier, 1790) 4

Glischrochilus sp. (Reitter, 1873) 7

Rhizophagus dispar (Paykull, 1800) 15

Quedius plagiatus (Mannerheim, 1843) 28 syn. Q.laevigatus (Gyllenhal)

Nudobius lentus (Gravenhorst, 1806) 10

Leptusa (Kraatz, 1856) 46

Leptusa cf pulchella (Mannerheim, 1830) (46?)

Phloeopora (Erichson, 1837) 1

Placusa (Erichson, 1837) 13

Phloeonomus (Heer, 1839) 824

Athous subfuscus (Müller, 1764) 9

Melanotus sp. (Eschscholtz, 1829) 5

Paraphotiscus impressus (Fabricius, 1792) 1

Denticollis linearis (Linnaeus, 1758) 1

Unknown/insignificant role

Rhyncolus ater (Linnaeus, 1758) 2

Enichmus cf rugosus (Herbst, 1793) 3

Cerylon (Latreille, 1802) sp. 2

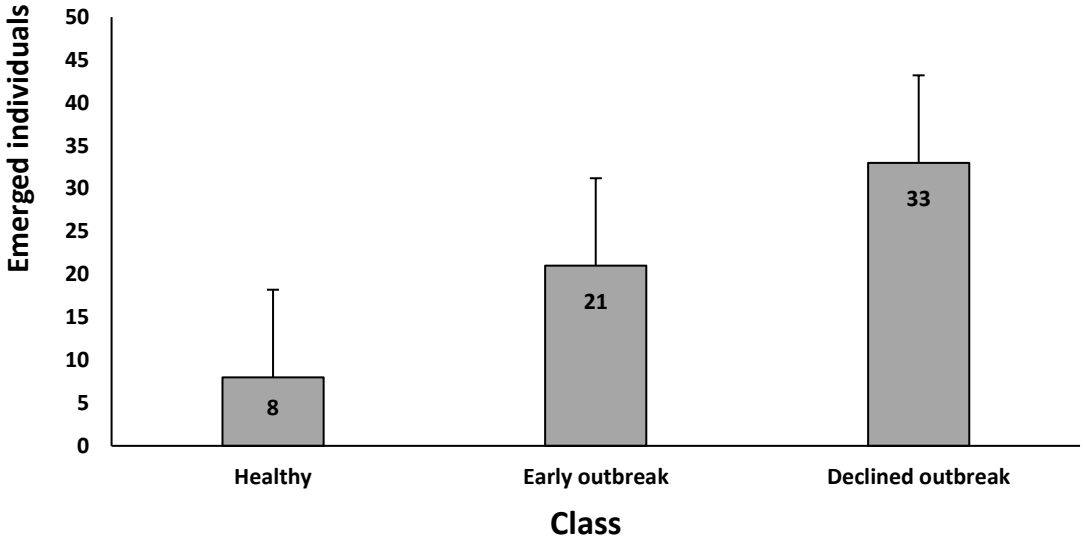
Ptiliidae (Heer, 1843) spp. 6

Appendix 2: Correlation tables for the three most common scolytids and nine antagonists in the current study. Spearman correlation was applied, with 0.05 level of significance (marked *, 0.01-level marked **).

		Ips typographus	Dryocoetes autographus	Crypturgus spp.	Thanasimus formicarius	Plegaderus vulneratus	Epuraea spp.	Rhizophagus spp.	Phloeonomus spp.	Nudobius lentus	Quedius plagiatus	Elateridae spp.	Pteromalidae spp.
Ips typographus	r_s	1.000	-0.030	0.462*	0.236	0.368	0.213	0.099	0.424*	0.207	0.218	0.040	-0.136
	p		0.882	0.015	0.236	0.059	0.286	0.624	0.028	0.299	0.275	0.844	0.497
Dryocoetes autographus	r_s	-0.030	1.000	0.097	0.404*	-0.146	0.192	0.100	0.573**	0.053	0.400*	0.324	0.369
	p	0.882		0.629	0.036	0.468	0.336	0.621	0.002	0.793	0.039	0.099	0.058
Crypturgus spp.	r_s	0.462*	0.097	1.000	0.089	0.293	0.174	0.289	0.196	0.197	0.054	-0.027	0.046
	p	0.015	0.629		0.659	0.138	0.386	0.143	0.326	0.326	0.789	0.892	0.821
Thanasimus formicarius	r_s	0.236	0.404*	0.089	1.000	-0.078	0.335	-0.015	0.483*	0.184	0.529**	0.409*	0.301
	p	0.236	0.036	0.659		0.697	0.088	0.939	0.011	0.358	0.005	0.034	0.127
Plegaderus vulneratus	r_s	0.368	-0.146	0.293	-0.078	1.000	0.465*	0.064	0.196	0.106	0.101	0.240	-0.006
	p	0.059	0.468	0.138	0.697		0.015	0.749	0.328	0.597	0.617	0.228	0.977
Epuraea spp.	r_s	0.213	0.192	0.174	0.335	0.465*	1.000	0.121	0.486*	0.265	0.223	0.465*	0.100
	p	0.286	0.336	0.386	0.088	0.015		0.549	0.010	0.182	0.263	0.014	0.620
N		27	27	27	27	27	27	27	27	27	27	27	27

		Ips typographus	Dryocoetes autographus	Crypturgus spp.	Thanasimus formicarius	Plegaderus vulneratus	Epuraea spp.	Rhizophagus spp.	Phloeonomus spp.	Nudobius lentus	Quedius plagiatus	Elateridae spp.	Pteromalidae spp.
Rhizophagus spp.	r_s	0.099	0.100	0.289	-0.015	0.064	0.121	1.000	-0.112	0.277	-0.264	-0.113	0.192
	p	0.624	0.621	0.143	0.939	0.749	0.549		0.577	0.162	0.183	0.574	0.339
Phloeonomus spp.	r_s	0.424*	0.573**	0.196	0.483*	0.196	0.486*	-0.112	1.000	0.243	0.462*	0.473*	0.082
	p	0.028	0.002	0.326	0.011	0.328	0.010	0.577		0.223	0.015	0.013	0.684
Nudobius lentus	r_s	0.207	0.053	0.197	0.184	0.106	0.265	0.277	0.243	1.000	-0.182	0.114	-0.154
	p	0.299	0.793	0.326	0.358	0.597	0.182	0.162	0.223		0.364	0.571	0.443
Quedius plagiatus	r_s	0.218	0.400*	0.054	0.529**	0.101	0.223	-0.264	0.462*	-0.182	1.000	0.222	0.235
	p	0.275	0.039	0.789	0.005	0.617	0.263	0.183	0.015	0.364		0.266	0.238
Elateridae spp.	r_s	0.040	0.324	-0.027	0.409*	0.240	0.465*	-0.113	0.473*	0.114	0.222	1.000	0.224
	p	0.844	0.099	0.892	0.034	0.228	0.014	0.574	0.013	0.571	0.266		0.261
Pteromalidae spp.	r_s	-0.136	0.369	0.046	0.301	-0.006	0.100	0.192	0.082	-0.154	0.235	0.224	1.000
	p	0.497	0.058	0.821	0.127	0.977	0.620	0.339	0.684	0.443	0.238	0.261	
N		27	27	27	27	27	27	27	27	27	27	27	27

Appendix 3: Cerambycid beetle *Rhagium inquisitor* between the stand classes. Opposed to other genera, these beetles did not emerge, but were instead found during debarking.



Appendix 4: Emerged pteromalid wasps between the stand classes.